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Bodily Symmetry: Origins and lifecourse associations with
cognition, personality, and status

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Declaration

I hereby declare that the thesis has been composed by me, that the work is my own except where clearly indicated, and that the work has not been submitted for any other degree or professional qualification. Information obtained from others is acknowledged in text and/or in the references.

David Hope

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Abstract

Bodily Symmetry: Origins and lifecourse associations with cognition, personality, and status

Symmetry – measured as the size asymmetry of a group of symmetrical body traits such as ear height or elbow circumference – has often been used as an index of the capacity to develop normally despite stress and correlates with a wide range of outcomes including intelligence, health and aspects of behaviour. However, theoretical debate continues over the underlying causes of these associations and outstanding methodological issues – such as the reliance on small sample sizes of college age students – makes the robustness of the findings uncertain. The present work advances the existing empirical literature in six separate domains. It also improves upon past methodology by using novel methods of digital measurement of asymmetry as well as for the first time digitally measuring endogenous asymmetry as indexed by the bones and linking bone asymmetry to intelligence. The research was conducted on four samples. Numbers given are for participants who provided asymmetry measures. Firstly, a sample of elderly participants from the Lothian Birth Cohort 1921 (LBC1921, $n = 216$) tested around ages 11, 79, 83, and 87. Secondly, the Science Festival Sample (SFS), a group of children recruited at a public science event aged between 4 and 15 ($n = 856$). Thirdly, a group of Orkney residents aged 18 to 86 (the ORCADES, $n = 1200$). Fourthly the Berlin Sample (BS), a group of Berlin residents ($n = 207$) between 20 and 30 years old. In the LBC 1921, men with poorer socioeconomic status in childhood had higher facial asymmetry in old age ($\beta = -.25, p = .03$). While investigating issues related to asymmetry in the same sample it was found that relatively more severe digit curvature – a minor physical anomaly – was associated with relatively greater cognitive decline ($\beta = -.19, p = .02$). Within the SFS asymmetry decreased across human childhood ($\beta = -.16, p = .01$), and more asymmetrical children exhibited slower choice reaction times ($\beta = .017, p = .002$). In the ORCADES sample, the more asymmetrical participants (as indexed by bone asymmetry) were less intelligent ($\beta = -.24, p = .01$). In the Berlin Sample and the LBC 1921 no consistent associations were found between personality traits and asymmetry. Collectively, these findings suggest symmetry functions as a measure of overall well-being as the trend is for higher asymmetry to be associated with a relatively poorer score on a variety of outcome measures. The findings considerably expand the number of existing studies in these empirical areas and in several cases – particularly asymmetry's association with socioeconomic status in the elderly and reaction times among children – represent the first work on those areas. The present work confirms the finding that asymmetry is linked to adverse outcomes. However, the underlying mechanisms by which symmetry is linked to such outcomes remain underexplored and require clarification.

Publications from this Thesis

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Contents

Declaration.....	2
Acknowledgements.....	3
Abstract.....	4
Publications from this Thesis.....	5
Contents	6
List of Figures	12
List of Tables	13
Chapter 1 – Symmetry: Definition, History, and Evolutionary Theory	15
1.1.1 Topics for Discussion	15
1.1.2 Symmetry Predicts Adverse Outcomes.....	17
1.2 Methodology: Measurement of Symmetry	18
1.2.1 Trait Selection and Aggregation	19
1.2.2 Different ways of Measuring Symmetry	19
1.2.3 Directional Asymmetry and Antisymmetry	22
1.3 Theoretical Explanations	24
1.4 Minor Physical Anomalies.....	25
1.5 Reporting on Symmetry	27
1.6 Symmetry across the Lifecourse	27
1.6.1 Empirical Findings: Symmetry across the Lifecourse	28
1.7 Symmetry, Cognitive Ability and Reaction Times	31
1.7.1 Empirical Work: Symmetry, Cognitive Ability and Reaction Times	31
1.8 Symmetry, Personality and Behaviour.....	35
1.8.1 Empirical Findings: Symmetry and Personality	37
1.8.2 Empirical Findings: Symmetry, Aggression and Cooperation	39
1.8.3 Empirical Findings: Symmetry and Mental Illness.....	41

1.9 Symmetry, Attractiveness, Sexual Behaviour, Fertility and Health	43
1.9.1 Empirical Findings: Symmetry, Attractiveness and Sexual Behaviour	44
1.9.2 Empirical Findings: Symmetry and Health.....	45
1.10 Symmetry and Early life Circumstances.....	47
1.10.1 Empirical Findings: Symmetry and Socioeconomic Status	48
1.11 Limitations in existing work	49
1.11.1 Sample Size.....	49
1.11.2 Diversity of Symmetry Measures and Methods.....	50
1.11.3 Failure to Control for Potential Confounds.....	50
1.11.4 Lack of Certainty over Sex Differences.....	50
1.12 Conclusion: The Usefulness of Symmetry Research	51
Chapter 2: Overview of Samples and Methods	53
2.1 Description of samples used in the empirical work	53
2.2 The Lothian Birth Cohort 1921.....	53
2.3 The Science Festival Sample	54
2.4 The Orkney Complex Disease Study	55
2.5 The Berlin Sample	55
2.6 The Measurement of Asymmetry across the Four Samples.....	55
2.7 Pre-existing Asymmetry Measures in the LBC1921	56
2.7.1 Digital Measurement of Facial Asymmetry in the LBC1921	56
2.7.2 Facial Asymmetry Outcome Measure.....	56
2.7.3 Physical Measurement of Bodily Asymmetry in the LBC1921.....	57
2.7.4 Digital Measurement of Hand Asymmetry in the LBC1921	58
2.7.5 Limitations of digital measurement in the LBC1921.....	61
2.7.6 Outcome Measure for bodily asymmetry in the LBC1921	62
2.8 Asymmetry in the SFS	62
2.8.1 Digital Measurement of Hand Asymmetry in the SFS	62

2.8.2 Limitations of Autometric.....	64
2.8.3 Outcome Measure of asymmetry in the SFS.....	64
2.9 Orkney Complex Disease Study	65
2.9.1 Digital Measurement of Bone Asymmetry in the ORCADES.....	65
2.9.2 Limitations of GIMP.....	67
2.9.3 Outcome Measure of asymmetry in the ORCADES.....	67
2.10 Improvements on previous methods of measuring asymmetry.....	68
2.11 Pilot Work: Remeasuring the LBC1921 handscans.....	68
2.12 Conclusions on Methodology	70
Chapter 3 – Overview of Empirical Chapters	71
3.1 Chapter 4 – Symmetry in Human Childhood.....	71
3.2 Chapter 5 – Symmetry and Intelligence.....	71
3.3 Chapter 6 – Symmetry and Reaction Times	72
3.4 Chapter 7 – Minor Physical Anomalies and Cognitive Decline	72
3.5 Chapter 8 – Symmetry and Personality.....	73
3.6 Chapter 9 – Symmetry and Socioeconomic Status	73
3.7 Summary of Empirical Work.....	73
Chapter 4 – Symmetry in Human Childhood.....	74
4.1 Introduction.....	74
4.1.1 Prior Research on Symmetry in Childhood	75
4.2 Method	76
4.2.1 Participants.....	76
4.2.2 Procedure	77
4.3 Results.....	78
4.4 Discussion.....	79
Chapter 5 - Symmetry and Intelligence	82
5.1 Introduction.....	82
5.1.1 Prior Research on Symmetry and Intelligence.....	82

5.2 Method	84
5.2.1 Participants.....	84
5.2.2 Apparatus and Procedure	85
5.2.2.1 Asymmetry.....	85
5.2.2.2 Intelligence.....	87
5.2.2.3 Covariates	88
5.2.3 Statistical Analyses	88
5.3 Results.....	89
5.3.2 Males.....	92
5.3.3 Females	92
5.3.4 Statistical Corrections	92
5.4 Discussion.....	92
Chapter 6 – Symmetry and Reaction Time	95
6.1 Introduction.....	95
6.1.1 Reaction Times and System Integrity	95
6.1.2 Empirical Research Linking Symmetry and Reaction Times	96
6.2 Study 1: Science Festival Sample from 2009	97
6.2.1 Participants.....	97
6.2.2 Apparatus and procedure	97
6.2.2.1 Asymmetry.....	97
6.2.2.2 Reaction times.....	98
6.2.3 Statistical Analyses	99
6.3 Results.....	99
6.4 Study 2: Science Festival Sample from 2010	102
6.4.1 Participants.....	102
6.4.2 Apparatus and procedure	102
6.4.3 Statistical Analyses	104

6.5 Results.....	104
6.5.1 Statistical Corrections	105
6.6 Joint Discussion of Studies 1 and 2	105
6.6.1 Links to Past Research	106
6.2 Strengths and Limitations of the Studies	107
Chapter 7 – Minor Physical Anomalies and Cognitive Ability	109
7.1 Introduction.....	109
7.1.1 Minor Physical Anomalies, Behaviour, and Mental Health.....	109
7.1.2 Minor Physical Anomalies and Intelligence	110
7.2 Method	112
7.2.1 Participants.....	112
7.2.2 Procedure	113
7.2.2.1 Cognitive Ability Test.....	113
7.2.2.2 Parental Education	113
7.2.2.3 Minor Physical Anomalies.....	113
7.2.2.4 Inflammatory Markers	114
7.3 Results.....	114
7.3.1 Statistical Corrections	119
7.4 Discussion	119
7.4.1 Findings in the Context of Past Research on MPAs and cognitive ability	120
7.4.2 Strengths and Weaknesses of the Study.....	120
Chapter 8 – Symmetry and Personality.....	122
8.1 Introduction.....	122
8.1.1 Personality and Fitness	122
8.1.2. The Present Studies.....	124
8.2 Study 1: Personality and Symmetry in the Lothian Birth Cohort 1921	125
8.2.1 Participants.....	125

8.2.2 Personality and Asymmetry assessments.....	125
8.3 Results.....	126
8.3.1 Statistical Corrections	127
8.4 Study Two: Personality and Symmetry in the Berlin Sample.....	130
8.4.1 Participants.....	130
8.4.2 Personality and asymmetry assessments.....	130
8.5 Results.....	130
8.5.1 Statistical Corrections	131
8.6 Joint Discussion of Studies One and Two	131
8.6.1 Strengths and Weaknesses of the Studies	132
Chapter 9 – Symmetry and Socioeconomic Status	133
9.1 Introduction.....	133
9.1.1 Socioeconomic Status: Measurement and Importance	133
9.1.2 Prior Empirical Work.....	134
9.2 Method	135
9.2.1 Participants.....	135
9.2.2 Procedure	136
9.2.2.1 Childhood Socioeconomic Status	136
9.2.2.2 Asymmetry measures.....	138
9.2.3 Statistical analysis	139
9.3 Results.....	140
9.3.1 Model fitting	142
9.4 Discussion	147
Chapter 10 – Discussion	150
10.1 Results.....	150
10.1.1 Asymmetry Scores	150
10.1.2 Symmetry across the lifecourse	151

10.1.3 Symmetry and Intelligence	152
10.1.4 Symmetry and Reaction Time.....	153
10.1.5 Symmetry and Minor Physical Anomalies	153
10.1.6 Symmetry and Personality	154
10.1.7 Symmetry and Socioeconomic Status.....	155
10.2 Summary of findings.....	155
10.3 Methodological Innovations	156
10.4 Limitations described in chapter 1	157
10.4.1 Sample Size.....	157
10.4.2 Diversity of Symmetry Measures and Methods.....	158
10.4.3 Failure to control for potential confounds.....	158
10.4.4 Lack of certainty over sex differences	159
10.5 Limitations in the present work	160
10.5.1 Limitations shared with past research.....	160
10.5.2 Range restriction	161
10.5.3 Range of symmetry measures	161
10.6 Future work.....	162
10.6.1 Further research within the existing samples.....	162
10.6.2 Further research on under-studied topics	163
10.6.3 Research on asymmetry measures	163
10.6.4 Research on the basis of the associations between asymmetry and well-being.....	163
10.7 Conclusions.....	164
References.....	165

List of Figures

Fig. 1.1 : Symmetry in humans and animals.....	17
Fig 2.1: Three digital hand scans	58

Fig. 2.2: Hand Asymmetry.....	60
Fig. 2.3: High zoom image of finger tip	61
Fig. 2.4: Autometric Interface.....	63
Fig. 2.5: Asymmetry of the bones.....	66
Fig. 2.6: Six measurers score symmetry of the hand	69
Fig. 4.1: Asymmetry decreases nonlinearly with age	79
Fig. 5.1: Full Body Bone Scan.....	86
Fig. 6.1: Deary-Liewald Reaction Time Task for Study 2.	103
Fig 7.1 – Low, Medium, and High Curvature of the Fifth Digit	115
Fig. 9.1: Models relating Early- and Mid-life Social status to Horizontal Facial Asymmetry at age 87, men and women combined (see text for explanation and table 9.3 for fit statistics)	145
Fig. 9.2: Models relating early- and midlife social status to Horizontal and Total Facial Asymmetry at age 87 in men only (see text for explanation and table 9.3 for fit statistics)	146

List of Tables

Table 5.1: Descriptive statistics and Correlation Matrix of Intelligence and Symmetry Variables	90
Table 5.2: Regression models predicting asymmetry	91
Table 6.1: Means and SDs for Reaction Time scores and models predicting asymmetry for Study 1 and Study 2	101
Table 7.1 - Correlation matrix of intelligence, curvature, mini-mental state examination score and inflammation	116
Table 7.2 - Linear regression models of Moray House Test IQ at age 79 and 87. Effects are given as B (SE), with standardised β below.	117
Table 8.1: Summary of Studies Examining Linear Associations of Asymmetry and Personality.....	124
Table 8.2 Linear regression models of asymmetry on personality score, adjusting for age and sex. Numbers are: B (SE), with standardised β below.	128
Table 8.3 Linear regression models of asymmetry on participant's deviation from mean personality score, adjusting for age and sex. Numbers are: B (SE), with standardised β below.	129

Table 9.1: Social Class (from childhood and participant's attained mid-life social class), crowding, number of occupants per household and access to toilet facilities.	137
Table 9.2: Correlation Matrix of Deprivation and Asymmetry variables.....	141
Table 9.3: Measures of Statistical Fit for Models Relating Early– and Mid-life Social status to Horizontal and Total Asymmetry at age 87 (see text and Fig. 9.1 and 9.2)	144

Chapter 1 – Symmetry: Definition, History, and Evolutionary Theory

All organisms contain a blueprint for their growth: organisms follow this plan throughout development, but do so imperfectly (Waddington, 1957). There is considerable interest in attempting to understand the causes of differences between the idealized blueprint and the resultant organism. Such differences may be caused by low precision in the capacity to follow the blueprint or stress across the lifespan. Understanding what specific factors cause such system-wide problems as increased susceptibility to illness may aid in the prediction and amelioration of problems across the lifespan and potentially contribute to policy aimed at reducing the effects of such problems. One marker that may index the sum of such problems in a given organism is symmetry (van Valen, 1962).

First fully described by Ludwig (1932), symmetry has received growing attention in the last half century due to widespread evidence that it correlates with important outcome measures across many species. Symmetry can be measured for any bilateral trait where symmetry is the normal developmental target. It is frequently measured in humans and nonhumans (Knierim et al., 2007); common examples are wing length, digit lengths or widths, ear size, and distances between landmarks of the face (Graham, Emlen, Freeman, Leamy, & Kieser, 1998; Palmer & Strobeck, 1986). See fig. 1.1 for examples. The greater the sum of the absolute deviations from equality, the lower symmetry is. Whether some traits are better or worse indicators of overall symmetry is an active area of debate (Banks, Batchelor, & McDaniel, 2010; Knierim, et al., 2007) and will be discussed extensively later (see chapter 1 section 1.1.2 for a review of existing methods, and chapter 2 section 2.2.3 for a full description of the methods used in this thesis).

1.1.1 Topics for Discussion

This review will discuss what symmetry is in animals and humans, current methods of measurement of symmetry and common topics for investigation. Symmetry research can be characterized as broad but shallow. Relatively few topics are repeatedly investigated: a recent meta-analysis of symmetry and intelligence (Banks, et al., 2010), one of the more heavily investigated areas, found only eight published studies on the topic.

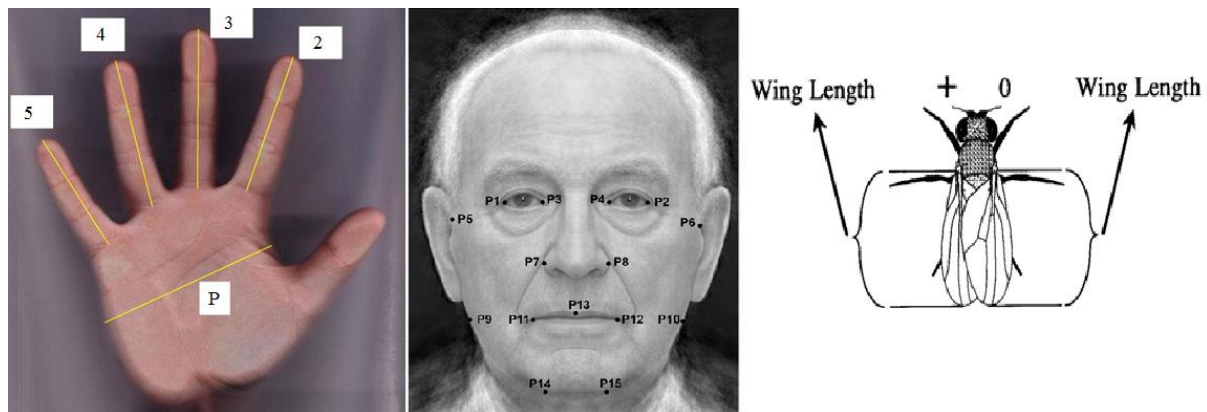
This review addresses current evidence across five major areas of considerable interest to researchers investigating individual differences in humans. Firstly, as ability varies across the

lifespan with many abilities peaking in adulthood and declining in old age (Craik & Bialystok, 2006), symmetry might also be expected to vary across the lifespan reaching an optimum in adulthood and then declining in old age. Secondly, it examines proposed links between symmetry and cognitive abilities. Intelligence and reaction time both predict longevity (Deary, 2008), so if symmetry indexes overall well-being high intelligence and fast reaction times should be linked to high symmetry. Thirdly, given that there is considerable interest in the causes of individual differences in personality and the fitness consequences of different personality traits (Gangestad, 2010), examining links between symmetry and personality and other behavioural variables may help explain the underlying causes of these differences. Fourthly, the review examines evidence linking symmetry to health, an important outcome measure that may determine the ultimate utility of symmetry as a concept. If symmetry is linked to health its utility in understanding lifespan development is likely to be strong. Lastly, given the evidence of the enduring effects of the early life period (Barker, 1995, 2007), the review will examine the extent which poor early life circumstances (such as socioeconomic status) has been linked to symmetry. Since a proposed cause of low symmetry is heightened stress during development symmetry should associate with early life circumstances. This review examines representative areas to illustrate the key goals, rather than describing every possible topic. For similar reasons it focuses primarily on humans.

Specific measurement methods are discussed in chapter 1, section 1.2. Here I focus on the empirical literature rather than the methodology. Briefly, the most common strategy for measuring symmetry is to aggregate as many individual traits as possible for a given organism (after standardizing for size) to best estimate symmetry at the level of the individual. Symmetry is useful as an indicator of early problems because the two bilateral traits present two attempts to produce the same item. That is, two index fingers are two attempts to follow the same plan of an index finger (Banks, et al., 2010; Bates, 2007). Therefore, it is possible that information about the relative inability to follow such a plan is informative of underlying problems with the organism: where one index finger is much larger than the other, the blueprint has not been followed well. In the literature the concept of symmetry is sometimes referred to as Fluctuating Asymmetry (FA) as the origins of these differences lie in deviations (fluctuations around) mean differences of zero (van Valen, 1962). Here the terms symmetry and asymmetry are both used. The positive term symmetry is used in conceptual discussions of the topic. Asymmetry, by contrast, is used to refer to the

measured outcome variable of a given study. The higher the asymmetry score, the relatively greater the size difference between traits. As most past research has used such a scale, with a higher number indicating a more adverse outcome, using the term asymmetry rather than symmetry for the outcome variable allows for consistency of reporting in comparison to past work, and indicates that, in the empirical work, the higher number on the asymmetry score should always be regarded as more adverse.

Fig. 1.1 : Symmetry in humans and animals



Note: From left to right: 1) Symmetry of the hand using five traits (digits 2-5 and breadth of the palm). 2) Facial asymmetry using paired landmarks (1 and 2 make up the first pair, 3 and 4 make up the second pair, and so on. 3) Symmetry of the wings of a fruit fly. Images are taken from van Dongen, Cornille and Lens (2009), Penke et al. (2009) and Van Valen (1962) respectively.

1.1.2 Symmetry Predicts Adverse Outcomes

Symmetry has been measured in, amongst others, humans, rhesus macaques, chickens, rabbits, rats, *Drosophila* and various species of fish (Knierim, et al., 2007; Palmer & Strobeck, 1986). The general trend is that across these and other species, lower symmetry (i.e. high asymmetry) is associated with higher levels of adverse outcomes across a wide range of characteristics (including outcome measures in all the domains discussed in section 1.1.1).

The empirical evidence that symmetry predicts poorer outcomes is robust, but there is disagreement of the underlying mechanisms that link low symmetry to these poor outcomes. Combined with the lack of a ‘canonical’ set of symmetry measures that could be used to

ensure reliability across studies, the utility of symmetry and its potential applications remain unclear despite its long standing usage (Banks, et al., 2010; van Dongen, 2011). Before examining the theoretical explanations for this trend, this review will examine existing methodology.

1.2 Methodology: Measurement of Symmetry

When conducting research on symmetry, four key issues must be considered. Firstly, given the relatively low level of asymmetry as a percent of trait size, the traits chosen for measurement may have an important impact on results. In particular, small traits may yield relatively higher rates of error in the measure of asymmetry. If the measurement tool is relatively imprecise small traits will have much greater error than large traits relative to the actual size, though this can be addressed by using large traits where possible or ensuring tools are as accurate as possible. Secondly, the method of measurement – which includes the use of physical measures such as callipers or tape measures or digital imaging – is important and may influence the comparability of the study with past research or the reliability of the measures. This can either be because different traits may be more accessible with different measures (it is easier to measure landmarks on the face with photography, for example, whereas it is difficult to do so with callipers), or because reliability may vary by the method used (Kemper & Schwerdtfeger, 2009) so differences in results may partially reflect differences of methods. Thirdly, the formula above is only valid if the developmental target is on average symmetrical: in some traits the developmental target is asymmetrical and therefore low symmetry is not informative of any underlying fitness which here refers to either greater health or greater likelihood of reproduction (van Valen, 1962). Means of detection and potential solutions involving statistical transformations, or selection of traits to avoid this “directional asymmetry” will be discussed in chapter 1, section 1.2.3 (van Valen, 1962). Finally, the asymmetry scores of individual traits tend to correlate poorly due to random effects on any given trait. Gangestad and Thornhill (1999) have suggested that the poor correlation between individual asymmetry scores of traits makes assessing any purported underlying fitness trait difficult when using just two data points (i.e. the left and right values of a trait): a single trait asymmetry score may have as little as 7% of its variance determined by the underlying fitness, even if fitness determines 100% of symmetry. Exceptions to this may exist. For example, in some cases traits very close together in the

body are likely to experience greater stress or injury simultaneously. Injury to a hand, or even a tendency to repetitively use that hand for many tasks, may cause higher wear or damage to all the bones of that hand therefore decreasing symmetry for all traits within the hand (assuming the undamaged or unused hand remains in its original state). For example, Livshits, Yakovenko, Kletselman, Karasik and Kobylansky (1998) found asymmetry scores in bones of the hands tended to be more highly correlated than was usual for traits. Asymmetry of any single trait is less informative than is an aggregate across multiple traits. Therefore, so far as is possible given time and resource constraints, more traits measured for asymmetry will improve validity though there is no consensus on the ideal number of traits (Knierim, et al., 2007).

1.2.1 Trait Selection and Aggregation

In humans common examples of traits used in symmetry research include finger lengths, ear size (usually height and width), circumference of the ankles and wrist, and landmarks on the face. For a more extensive list discussing non human species see e.g. Palmer and Strobeck (1986). While the factors described above are important, trait selection often appears to reflect convenience and ease of measurement (Banks, et al., 2010; Palmer & Strobeck, 1986) and so different areas of research may use different symmetry measures.

Aggregation of traits can be approached in different ways. The most common method is to calculate a mean asymmetry score from all the individual traits for easy comparisons with previous work, though alternatives such as constructing a latent trait out of the individual measures may be equally feasible. Little empirical evidence exists comparing such methods though some studies have attempted to use factor analysis to identify asymmetry (Graham, et al., 1998). There is no agreed set of measurements that maximizes validity, and it is typically assumed that all traits are equally informative with respect to symmetry. The diversity of asymmetry indexes is high but with a sufficient number of items any set of traits should be equivalent to any other set of traits.

1.2.2 Different ways of Measuring Symmetry

The second major issue to address concerns the method of measurement. Modern techniques may provide better results than more long-standing methods due to the higher quality of recording with digital photography and scanning. On the other hand, the comparability of

new methods with old is not clear. The equivalence of the major approaches has rarely been explicitly examined, and practical concerns such as the traits to be measured, and the resources available, may be important factors as well.

The most well established method is to measure the traits physically in person. Typically done with callipers or a tape measure, this involves a tester measuring the desired traits of the participant with tools of an appropriate level of accuracy: usually 0.1 mm or better. For an example see e.g. Prokosch, Yeo and Miller (2005). Given the potentially high level of error due to the relatively small size differences being measured, training is essential. Reliability can be improved in several ways. Firstly, measurements for each trait can be taken two or three times and averaged. Secondly, several independent raters can measure each trait and the degree of concordance analyzed.

Using physical measurement has several advantages. Given its long standing usage a study utilizing the technique can easily be compared to prior research. It is often a convenient technique when participants need to be present to give other measures such as blood pressure or height. However, there are disadvantages. The participant must be present throughout the procedure. This may be time consuming if there are many traits to be measured, especially when each trait is repeatedly measured for accuracy. At least one study found participants were uncomfortable with the measurement process itself (Waynforth, 1998). Possible errors identified in the raw data can only be checked by recalling the participant. Some researchers have expressed concern that handedness of the measurer may introduce systematically higher error for one side of the body than the other according to the measurer's preferred hand allowing for greater accuracy for one side than the other (Johnson, Segal, & Bouchard, 2008).

Increasingly in the last two decades digital photography and other forms of imaging have been used for reasons of practicality and reliability (Kemper & Schwerdtfeger, 2009). Digital images are easily obtainable for hands, faces, and can often be conveniently acquired from body or brain scans where the output is digital as opposed to hard copy. The participant needs to be present for the image capture, but not the measurement of the traits, and consequently there can be less of a draw on the participant's time. Given modern high-resolution images, asymmetry can be measured to a very high degree of accuracy with digital software. Advantageously, colour contrast magnification and orientation can be varied to boost the clarity of the image, allowing for higher accuracy. Given that the interface (usually a

keyboard and mouse) is identical for all measured traits, handedness of the measurer should not be an issue. Furthermore, combined with tools designed to image internal structures – x-ray scanners for example – traits which are simply inaccessible to physical measurement (or accessible only post-mortem) may be available for use. Notably, as the original digital image or photocopy remains available, any errors found during analysis can be rechecked without having to recall the participant. While relatively little empirical data is available on the subject, Kemper and Schwerdtfeger (2009) suggest that digital measurement is preferable to physical measurement due to the capacity for much higher accuracy, although it takes slightly longer to score digital images.

Symmetry has most commonly been scored in the literature via the following formula:

$$2(L-R)/(L+R)$$

Here L = the left trait, and R = the right trait. Multiplying the result by 100 gives a percentage score. Zero indicates perfect bilateral symmetry and most traits exhibit asymmetries of around 1% or less (Lens, Van Dongen, Kark, & Matthysen, 2002). This will be referred to hereafter as the ‘symmetry formula.’ Where studies have used a different method for calculation it will be noted in text.

Whether captured physically or via an image, asymmetry is measured by recording the length of the left and right version of the trait and then calculating the size difference using the formula described above. This is applicable in most cases, though there are exceptions. One exception, for which several alternative strategies have been developed, concerns measurement of the face. The face can present challenges as it tends to possess landmarks rather than traits with an easily identifiable length or circumference. After taking photographs under carefully standardized lighting conditions and excluding those with tilt or obscured features (typically due to hair), the rater uses some form of imaging software to measure asymmetry. First, the face is aligned so that a vertical line is drawn through the average midpoint of all the landmarks. Asymmetry is then calculated by comparing the left and right trait’s distance to this central midline, rather than the distance between each other. Common examples include corners of the mouth, the outside of the eyes, and the edges of the chin. Full details of this type of procedure can be found in Grammer and Thornhill (1994). However,

the face is one trait where directional asymmetry is especially problematic, so additional work (described later in this section) is necessary to ensure the asymmetry measure is valid.

This procedure requires a rater. One relatively new technique, typically used with facial imaging though in theory of wider applicability, is digital image analysis. The image capture process is the same as for digital photography: only the method of measurement is different. While a rater is needed to evaluate images in terms of quality (poor lighting, tilt, or hair obscuring features means the image cannot be measured) the process of examining asymmetry is automated. Rather than taking the entire face, a rectangle using the outer eye corners, the top of the brow and the bottom lip is selected from the image. Then the entire rectangle is divided into 1 pixel wide sections and the difference between the left and right half of the face is calculated as the difference between the total number of pixels of the left and the total number of pixels of the right half of each section. This is repeated for all sections. The minimum difference between the left and right total gives the asymmetry point. An asymmetry index can be calculated as the length of the line joining the symmetry points divided by the total height of the rectangle. An example of this procedure can be found in Fink, Neave, Manning and Grammer (2005). This process is advantageous as it requires relatively little effort on the part of any rater and is not subjective. However, it excludes peripheral regions of the face and, as the process depends on colour contrast, may falsely estimate asymmetry as a result of lighting asymmetry (Pound, Penton-Voak, & Brown, 2007), whereas a landmark based system avoids this issue.

1.2.3 Directional Asymmetry and Antisymmetry

A complicating factor in the measurement of symmetry is that not all traits have symmetry as their ideal developmental target. Two other forms of asymmetry – directional asymmetry (DA) and antisymmetry – can make use of the formula described above inaccurate as the presence of these two additional variables inflates the asymmetry score despite providing no indication that the developmental target has been missed.

Directional asymmetry is where there is a tendency for one side of the trait to be larger than the other across the population. This can be the ideal developmental target such as in the heart (van Valen, 1962) or brain (Palmer, 2004) of a mammal or as a consequence of greater usage of one side of the body over the other. As such it is sometimes argued that humans may

exhibit directional asymmetry as a consequence of their handedness (Johnson, et al., 2008). Faces are also known to demonstrate high levels of directional asymmetry and so when scoring symmetry for facial traits, correction for DA is necessary to avoid error (Grammer & Thornhill, 1994).

Multiple tactics have been identified to deal with this issue. Detection is relatively simple: in an acceptably large sample there should be no size differences between the left and the right side of the trait if directional asymmetry is not present. Consequently a t-test provides a simple means of assessing directional asymmetry. One common strategy for dealing with directional asymmetry involves subtracting the average L-R differences from each score on the side with the larger mean value (van Valen, 1962). However, this may still result in overestimates for asymmetry if directional asymmetry varies across individuals in the sample. One alternative technique involves regression. Here, a regression slope is estimated with the geometric mean of the slope from the left traits on the right traits and the inverse of slope of the right traits on the left traits. The standardized residuals from this procedure record asymmetry (Johnson, et al., 2008). Another tactic, commonly applied to directional asymmetry of the face, involves principal components analysis. Under principal components analysis, two components are identified: the first indicates DA, and the second indicates asymmetry (Simmons, Rhodes, Peters, & Koehler, 2004). Alternatively, given that all these strategies involve estimates and some traits appear not to exhibit directional asymmetry, some researchers have recommended excluding traits which exhibit high directional asymmetry as the most straightforward and valid option (Knierim, et al., 2007).

Antisymmetry, by contrast, exists where there is a strong preference for one trait to be much larger than the other but there is no preference for which side is larger (van Valen, 1962). Where this is present in a trait there is typically a bimodal distribution of scores. This can be tested for via kurtosis of the signed asymmetry and traits with antisymmetry are usually excluded (Knierim, et al., 2007). In practice, for human samples directional asymmetry is much more common than antisymmetry and many studies of human samples do not report antisymmetry tests.

1.3 Theoretical Explanations

Symmetry is linked to a wide range of adverse outcomes (Knierim, et al., 2007; Møller, 2006; Van Dongen & Gangestad, 2011) across a diverse range of measures. The theoretical basis for the relationship between symmetry and adverse outcomes (discussed fully in chapter 1 sections 1.6-1.10) remains an area of active debate. This section will describe the most commonly agreed upon explanation, a potential alternative, and how such theoretical explanations can be tested and applied.

The most widely held and longest established theory to explain the association between symmetry and poorer outcomes is that symmetry is an indicator of underlying fitness (van Valen, 1962). Specifically, symmetry is thought to index (rather than cause) developmental instability, which can be thought of as a measure of fidelity (Waddington, 1957). The more able the organism is to ‘implement’ its genotype in the environment, the fewer random errors there will be. As symmetry measures random errors across the body, low instability should lead to high symmetry. On the other hand, organisms who have a low capacity to resist stress, or those who experience more stressors throughout the lifespan, will experience greater difficulty implementing their ‘plan’ and consequently exhibit higher asymmetry. An alternative way of conceptualizing the relationship between symmetry and well-being is via the concept of ‘system integrity’. System integrity is regarded as a latent trait which measures how well the organism is built or how well functioning it is (Whalley & Deary, 2001). System integrity has attracted considerable interest in recent years as a potential explanation for the tendency for cognitive and physical capability to decline simultaneously (Deary, 2008) though the theory remains relatively untested and vague (Gale, Batty, Cooper, & Deary, 2009). This prediction can be tested by examining links between symmetry and well-being (cognitive as well as physical): if symmetry is not indicating system integrity then no associations between symmetry and well-being should be found.

However, at least one major alternative exists to the proposal that symmetry indexes system integrity. This alternative states that symmetry does not measure integrity and symmetry instead is directly informative via two mechanisms: lateralization and direct effects of asymmetry (van Dongen, Cornille, et al., 2009). Firstly, lateralization leads to the left and right sides of the body being used to a different degree so high asymmetry may simply reflect the degree of lateralization and consequently symmetry reflects lateralization (and its

associated outcomes) rather than system integrity. Systematic usage of one side over the other is directional asymmetry rather than asymmetry as discussed here, but a failure to correct for directional asymmetry – common in many studies – may mean asymmetry from lateralization is erroneously recorded as meaningful, random asymmetry (Özener, 2010). Secondly, symmetry may have direct consequences for fitness rather than indexing system integrity if organisms have a tendency to prefer the more symmetrical (van Dongen, 2011). While this model does not mean symmetry is uninformative, it requires a substantially different interpretation of the causal mechanisms of the empirical findings as symmetry may not be indicating an underlying trait, and consequently at least some of the attempts to link symmetry to overall fitness may be incorrect. Such models can be tested by exploring changes in asymmetry over time (only directional asymmetry should increase over time in this model, not conventional asymmetry) or examining links between symmetry and attributes where the preferences of others do not appear meaningful (such as empirically measuring physical well-being or reaction times).

Both of these issues will be discussed where relevant in the empirical sections (chapter 1 sections 1.6-1.10). Before discussing the empirical work on symmetry, it is important to examine one more topic. Given the evidence that using more measures of symmetry improves reliability (Knierim, et al., 2007) and that individual indicators of underlying well-being index it only poorly (Gangestad & Thornhill, 1999), using multiple measures is essential for establishing the validity of a study. However, increasing the number of symmetry measures is only one solution – an alternative is to also examine other indicators of underlying problems. This review will now examine a second such indicator: Minor Physical Anomalies (MPAs).

1.4 Minor Physical Anomalies

MPAs are small, distinctive bodily features which do not impair everyday functioning. However, they may indicate a congenital disorder (Compton & Walker, 2009) or stress accumulated over the lifespan (Flatt, 2005).

Anomalies are diverse in nature and occur all over the body. The earliest scale to describe MPAs – the Waldrop scale (Waldrop, Pedersen, & Bell, 1968) included a series of these. Examples include multiple hair whorls or crowns (most humans exhibit only one), malformed ears, a steeped palate, an inward curving fifth digit on the hand or syndactylia of the toes.

These traits are categorized as anomalous only where they are distinctively different from the equivalent trait in the normal population (Waldrop, et al., 1968).

Measurement usually occurs via a trained rater checking all the sites of interest. For convenience, sites used in a study may be restricted to an accessible body part (such as the craniofacial region) or cover the entire body. Several scales exist, and as in symmetry research, there is no consistent agreement on whether some traits are preferable to others although some research suggests some MPAs are more likely to be present in the aged (Lloyd, Doody, Brewin, Park, & Jones, 2003) and therefore potentially problematic when comparing age groups.

MPAs are positively associated with a number of issues such as Down's syndrome (Waldrop, et al., 1968), changes in emotionality (Paulhus & Martin, 1986) and schizophrenia (Compton & Walker, 2009). These issues will be taken up in further detail in the appropriate empirical sections of this review. The key point here is that MPAs appear linked to serious conditions and behavioural variables in the same way as symmetry. Given that some aspects of symmetry measure similar physical traits it is possible to test symmetry at the same time as MPAs. The purpose of including MPAs in the present review is to demonstrate that measurement of symmetry and MPAs in a single session may greatly improve the design of a study. If both symmetry and MPAs indicate underlying integrity, reliability will be increased by including measures of both in a single study. Notably, if MPAs predict the same outcome variables as symmetry, it would be implausible to suggest symmetry correlates with positive outcomes solely due to lateralization or a residual preference for symmetry (van Dongen, 2011) as MPAs would not be expected to be associated with either.

Relatively few studies examine MPAs and symmetry simultaneously. Much of the work that does exist is closely tied to mental illness (especially schizophrenia) which is where much of modern MPA research occurs. However, at least some examples demonstrate a relationship between the two areas. Weinstein, Diforio, Schiffman, Walker and Bonsall (1999) found that, in 20 schizophrenics, the number of MPAs correlated positively and significantly with high asymmetry ($r = .23$). Given the indication that a single symmetry trait will not predict underlying integrity well expanding indicators of integrity to include MPAs may be one means to improve the quality of research.

1.5 Reporting on Symmetry

The next five sections describe empirical work linking symmetry to adverse outcomes across the domains outlined in section 1.1.1. The main focus throughout is the data, though theoretical explanations for such links will be discussed where appropriate. The studies are primarily taken from research conducted in the last fifty years and as such a variety of different reporting styles have been used, and in many cases the statistics reported vary from study to study. Some, for example, do not report sex-specific age means and SDs, while others provide only a range for the whole sample age. Wherever possible, sample size, number of males and females, the mean and SD of age and effect sizes are reported. The method of obtaining asymmetry is reported along with the number of traits where appropriate. It is conventional in the literature to report outcome measures as an asymmetry score, with zero indicating perfect symmetry and a higher number indicating a poorer outcome (van Valen, 1962). This convention is followed here. As such, where relationships are reported, an asymmetry score is used in all cases. A negative correlation between asymmetry and intelligence, for example, would indicate higher asymmetry was associated with lower intelligence. The review of the empirical work will begin by examining asymmetry in relation to age.

1.6 Symmetry across the Lifecourse

While symmetry may indicate underlying well-being, it is not the only attribute to do so. Importantly, many variables relevant to health and well-being follow a trajectory across the lifespan whereby they approach their optimum state in early adulthood then remain stable until late midlife, whereupon they begin to decline. This pattern is commonly observed in cognition: fluid abilities increase into adolescence, but decline in late life (Craik & Bialystok, 2006). One way of evaluating whether symmetry is related to system integrity is to test for associations between symmetry and other potential indicators of integrity, a prospect that will be taken up in more detail elsewhere. A second method is to examine symmetry across the lifecourse. Given the well described trend for abilities across many domains to optimize at adulthood and decline in late life (following a u-shaped curve), if symmetry is an indicator of underlying system integrity it might also be expected to follow such a curve. Evaluating the relationship between symmetry and age is therefore a promising means of evaluating its utility and the underlying relationship between symmetry and the outcome variables

discussed here. If symmetry is measuring underlying bodily system integrity symmetry should vary across the lifecourse. Either it should increase linearly as a sign of accumulating stressors that occur with age. Or it should vary up and down according to present level of stress on the organism, with active symmetry enhancing mechanisms working to increase symmetry where possible. The latter prospect is especially relevant as an investment of resources in optimizing symmetry would demonstrate symmetry's evolutionary significance, and that there are good reasons to expect the variable to be meaningfully informative of status and for this indicator to be interpreted by others as being informative of status. Alternatively, if symmetry is a byproduct of lateralization or a preference for symmetry and so uninformative of system integrity (van Dongen, 2011) symmetry should not vary across the lifespan in the same manner as other (e.g. cognitive) variables. Symmetry should be uninformative of changes in the state of the organism across the lifespan.

1.6.1 Empirical Findings: Symmetry across the Lifecourse

Despite the potential for research on age and symmetry to clarify the theoretical importance of symmetry, very little work has been conducted on the subject. There is a tendency (which will be highlighted throughout this review where appropriate) for symmetry research to focus on college age participants with relatively small sample sizes. Comparisons of symmetry across the lifespan are difficult to obtain and most studies that record age generally have too small of an age range to provide meaningful inferences. Several studies have recorded age as part of their analysis without making it a focus of their research.

Gangestad, Thornhill and Yeo (1994) tested 72 college students (37 men, and 35 women) with a mean age of 23.2. Asymmetry was measured for seven bodily traits, and after controlling for sex higher asymmetry was significantly correlated with age ($r = -.20$). On the other hand, a later study by the same author using a much larger sample size found no relationship between age and asymmetry. Gangestad and Thornhill (1997) tested 203 heterosexual couples (equal numbers male and female) with a mean age of 21.1 ($SD = 3.6$) for the men, 20.0 ($SD = 3.2$) for the women. Using between seven and nine bodily traits for asymmetry, they found that asymmetry did not correlate significantly with age for males ($r = -.09$) or females ($r = -.01$). These are representative of an inconsistent trend in narrow age cohorts. Investigation the issue in college age samples, given the age restriction, is

problematic and sample sizes are low by the standards suggested by Van Dongen and Gangestad (2011).

However, two studies have examined age and symmetry using samples that are informative of the basis of symmetry. The first of these (Kobyliansky & Livshits, 1989), examined symmetry as part of a large scale cross-sectional study of an Israeli population. Examining eight symmetry traits with a total n of 2213 ranging from neonates to the elderly (age 75-94), they identified that the elderly group had significantly higher asymmetry than the younger groups. This provides support for the idea that asymmetry increases as a result of the stressors experienced across the lifecourse: if symmetry were uninformative, it would not vary over time in response to life stage. This study also demonstrates the use of attaching symmetry research to large cohorts which have been examined for a variety of medical and demographic traits: a much larger sample size is thereby obtainable and it is possible to then more easily examine links between symmetry and a range of variables. This issue will be addressed in more detail later. As an aside, there is (albeit very limited) evidence that the incidence of some MPAs increase with age (Lloyd, et al., 2003) which may reflect the same underlying trend of bodily deterioration being reflected by indicators of integrity.

A second study provides further useful information on the relationship between symmetry and age. Wilson and Manning (1996) conducted a cross-sectional study of 680 participants drawn from a geographically narrow area – the city of Liverpool, UK – with a broad range of socioeconomic backgrounds. They examined 40 participants each from the age of two to the age of eighteen, with 20 male and 20 female per age band. Measuring asymmetry via eleven bodily traits, they found that asymmetry declined across the measured time period. However, the relationship was not linear: asymmetry did not decline during the 11-15 period, where there was instead an increase in asymmetry. A cubic polynomial regression best modelled the data. Importantly, this trend suggested that asymmetry decreased except during the period when the children were undergoing the adolescent growth spurt (Bogin, 1997). This suggests that the capacity to maintain symmetry is influenced by the state of the organism: during energy intensive or stressful periods (such as the growth period) it is harder to maintain symmetry. Furthermore, there are active processes increasing symmetry present at least during human childhood. The optimization of symmetry supports the proposition that symmetry is an important indicator of system integrity and optimizing symmetry has

advantages for the organism, and that the symmetry of the organism may be monitored by other members of its species.

This suggests additional advantages to investigating symmetry. Changes in symmetry over time may indicate shifts in life status. A rise in symmetry indicate improvement in circumstance, reductions indicate problems. However, existing research is limited in several important respects. Most importantly despite the potential importance of the topic very few studies have examined the relationship between symmetry and age in large samples with a cross section of ages. More research is needed to ensure the findings are robust. Secondly, the existing research does not describe participants who are followed across multiple waves. That is, participants were not measured repeatedly over an interval of several years. While such a design is undoubtedly resource intensive, it would provide extremely valuable information on changes in symmetry with age. At present the research only informs us of differences in symmetry across different age bands, so it is not known whether these findings will be true when measuring the same individuals repeatedly. Examining individuals repeatedly across time would be a major improvement to the existing work.

The research on symmetry across the lifecourse has implications for how symmetry research in general should be conducted. It strongly suggests age is an important covariate that may influence the relationship between symmetry and outcome variables of interest. If the age range is dispersed in a study but age is not controlled for, the resultant analyses may be flawed as any characteristic that varies with age may appear to vary with symmetry simply because symmetry is declining with age. Alternatively, if symmetry is varying across the lifespan in response to different pressures – with symmetry reaching its optimum state as the individual enters its reproductive phase then comparisons between narrow age samples of different studies may be problematic.

Given the association between symmetry and age, and the apparent, albeit very limited, evidence that it follows the same trajectory of many abilities across the lifecourse, it is logical to next examine a series of linked abilities for which the lifespan trajectory has aroused considerable interest. This review next examines links between symmetry and cognitive ability.

1.7 Symmetry, Cognitive Ability and Reaction Times

Cognitive abilities have been extensively studied in psychology, and there is considerable interest in explaining both individual differences in cognitive abilities and changes in those abilities over the lifecourse (Craik & Bialystok, 2006; Deary, 2008). Some researchers have proposed that intelligence, along with Reaction Times (RTs), predict mortality so well because they are indicators of underlying system integrity and therefore can be used to assess the well-functioning of the organism (Deary & Der, 2005a; B. A. Roberts, Der, Deary, & Batty, 2009). There are good reasons, then, to expect symmetry to correlate with RTs and intelligence, and the existence of such a relationship may shed considerable light on the underlying individual differences in ability and demonstrate the utility of symmetry in psychological research.

While the relationship between cognition and symmetry is one of the more thoroughly studied areas of symmetry research, there are still relatively few studies in total and the tendency to rely on small, college age samples remains problematic. The discussion here focuses on intelligence research, with attention also drawn to three studies which tested RTs alongside measures of intelligence.

1.7.1 Empirical Work: Symmetry, Cognitive Ability and Reaction Times

The first study on the topic (Furlow, Armijo-Prewitt, Gangestad, & Thornhill, 1997) tested 240 undergraduate students across two studies (97 male, 143 female, mean age for study 1 22.6, for study 2 21.1). Asymmetry was measured via nine traits of the body. Participants completed a measure of Cattell's culture fair intelligence test: higher asymmetry was associated with lower scores on the intelligence measure across both studies (β of $-.17$ and $-.26$ for study 1 and study 2 respectively).

Subsequent research has replicated and, to an extent, expanded on this finding. Rahman, Wilson and Abrahams (2004) tested links between symmetry and intelligence in heterosexual and homosexual males and females. Of the 240 participants, a quarter were heterosexual males (age $M = 29.9$, $SD = 6.6$), a quarter homosexual males (age $M = 32.1$, $SD = 5.7$), a quarter heterosexual females (age $M = 26.8$, $SD = 5.9$) and a quarter homosexual females (age $M = 29.6$, $SD = 5.4$). The study used two traits for asymmetry, and measured intelligence via mental rotation, judgement of line orientation, letter fluency, category fluency, synonym

fluency, digit-symbol substitution and object location memory. No results were significant for women. Among heterosexual men there was an association between judgement of line orientation and asymmetry. For homosexual men, there were associations between asymmetry, letter fluency, category fluency, synonym fluency, and digit-symbol substitution. The relationships were in the expected direction with higher asymmetry associating with lower intelligence. Effect sizes (r) were between $-.29$ and $-.36$. This is the only study to indicate potential differences based on sexuality. Note, however, that the sample size was very small in comparison to that proposed by Van Dongen and Gangestad (2011) and while the participants were older than those in the Furlow et al. study, they were still relatively young.

Prokosch (2005) tested 78 males (age $M = 21.5$, $SD = 6.1$) on 10 bodily asymmetry traits. The goal was to test the relationship between cognitive ability tests which loaded on to general intelligence: as different tasks of cognitive ability reflect general intelligence to a different degree, symmetry would be expected to associate mostly strongly with those that loaded highly on to a measure of general intelligence. Intelligence measures included a Raven's Progressive Matrices Test (RPMT), two vocabulary tests, and two digit-span tests. Higher asymmetry associated significantly with slower completion of RPMT ($r = -.39$), with one vocabulary test performed significantly worse by those with high asymmetry ($r = -.25$) and no significant associations with digit-span. Given that RPMT was proposed as the task most highly associated with general intelligence, this supports the suggestion that symmetry relates to general intelligence. High asymmetry was associated with slower completion time for all significant results.

Thoma et al. (2006) tested 21 right handed adult males (age $m 24.3$, $SD = 2.7$). Participants were tested for six bodily symmetry traits, and performed a RPMT. Symmetry was significantly associated with performance on the RPMT, despite the extremely small sample size; those who completed the task slower had higher asymmetry ($r = -.49$). This study is notable for its focus on male participants only. The cause of this will be discussed in more detail later.

A similar study was conducted by Luxen and Buunk (2006), who tested 81 participants of which 44 were males (age $M = 21$, $SD = 2.8$) and 37 females (age $M = 20$, $SD = 3.6$). Asymmetry was assessed by five bodily traits, and intelligence was measured as a Principal

Component Analysis on a RPMT, a numerical test and a verbal test of reasoning.

Asymmetry significantly predicted intelligence ($r = -.25$) for both males and females.

Bates (2007) tested symmetry and intelligence across two samples. The first comprised 98 participants of which 32 were male (age $M = 32.1$, $SD = 11.1$) and 66 female (age $M = 31.5$, $SD = 14$). Asymmetry was measured via nine traits, and intelligence was measured via a RPMT. High asymmetry was associated with low intelligence ($r = -0.43$). This was replicated in the second study of 164 participants, of which 40 were male (age $M = 21$, $SD = 7.5$) and 124 were female (age $M = 21.6$, $SD = 7.3$). Asymmetry was measured in four bodily traits, and intelligence was measured with RPMT and again high asymmetry was associated with significantly lower intelligence ($r = -.29$).

Johnson, Segal and Bouchard (2008) tested the relationship between symmetry and intelligence in a sample of twins. They tested 263 individuals including 88 pairs of twins (age $M = 47.8$, $SD = 12.9$). Using 10 bodily asymmetry traits, and intelligence as measured by the Wechsler Adult Intelligence Scale, they found no association between intelligence and asymmetry. In addition to being the first null result published, this paper used a much larger sample size with a much higher mean age than any preceding study, and was able to examine potential correlates in the genetic influence of symmetry and intelligence.

The most recent study, Penke et al. (2009), tested links between symmetry as measured in the face and a variety of cognitive measures in a narrow age cohort (age $M = 83$, $n = 216$). Unlike previous studies, intelligence measures were available from several points in the lives of the participants (including childhood), and so in addition to testing intelligence (as measured via the first component of a PCA of verbal fluency, a RPMT and a logical memory test) it also measured cognitive decline between the ages of 11, 79 and 83. It is the only study here described to test change in cognitive ability. For women, no significant associations were found between asymmetry and intelligence or change in intelligence. In men, change in intelligence between age 79 and 83 was significantly associated with high asymmetry ($r = -.35$), but intelligence at 11, 79, or 83 was not associated with asymmetry.

A meta-analysis of these studies (and several more that were unpublished) supported the general trend (Banks, et al., 2010) with the effect size between asymmetry and intelligence across the studies being around $-.16$. The meta-analysis highlighted several outstanding issues

which are shared by much of symmetry research. The sample size tends to be low in most studies, the traits used are inconsistent and follow no fixed pattern, there is little accounting for potential confounds such as age, and there is little attempt to address the possible sex differences. Note, for instance, that while Penke et al. found a significant association in men only, and Thoma et al. did not test women at all, Luxen and Buunk found both men and women exhibited the relationship between symmetry and intelligence.

Of the described studies, two also tested RTs. RTs are a basic measure of information processing that associated with intelligence; faster reaction times are associated with higher general intelligence (Jensen, 1982). Two studies examined links between symmetry and RT. Thoma et al. (2006) found that participants were slower on a RT task if they were more asymmetrical, for both simple and choice tasks. Secondly, Penke et al. (2009) in addition to measuring intelligence, tested associations between both simple and choice RTs and symmetry. Again, males exhibited slower and more variable choice RTs ($r = .30$ and $.21$ respectively) when they were more asymmetrical. No relationship was found for females. Neither sex showed any association between symmetry and simple RTs.

Combined, these RTs findings support the proposal that there are links between cognitive ability and symmetry. The fact that RTs are a basic measure of information processing suggests that the links should relate to all forms of cognitive ability, not just complex reasoning tasks. However, as with the intelligence research, the work is in some respects limited. Only one study tested women, and more replications are needed to be confident of the results. Again, neither study meets the criteria suggested to ensure high power for the anticipated effect sizes (Van Dongen & Gangestad, 2011).

Of the studies described here, four use samples with a mean age of under 25, with one more using a sample with a mean age in the low 30s. Only one has studied the elderly, and only this study tests changes in cognitive ability over time. As such, while the existence of a link between symmetry and cognitive ability is well documented, its causes, potential confounds, and relationship to change within a person over time, remains almost entirely unstudied.

A parallel set of work has investigated cognitive ability in relation to MPAs, though few studies have been conducted. Rosenberg and Weller (1973) found that among 99 children (age approximately 7), higher MPAs were significantly associated with poorer verbal

intelligence, and children with a high number of anomalies were more likely to repeat the academic year. Pine, Shaffer, Schonfeld and Davies (1997) replicated this finding in a further 118 male participants (also aged approximately 7 years old), with participants with more MPAs exhibiting lower verbal intelligence. Gally, Kantola-Sorsa and Granström (1988) found that, in a comparison of 108 children of epileptic mothers and 100 control children, higher MPAs in both groups were related to lower performance on measures of general intelligence.

Two other studies are worth noting. Firstly, one study reported a null result (Marcus, Hans, Byhouwer, and Norem, 1985) but argued this was derived from the very low sample size. One other study (Dimambro et al., 2008) tested the level of MPAs in 186 adults with a first-onset psychotic disorder as opposed to 145 controls. Higher numbers of MPAs were associated with lower premorbid intelligence ($r = -.12$) and current intelligence ($r = -.19$).

As such there is some evidence that intelligence is negatively associated with greater number of MPAs. Notably, the sample types differ from that typically used in symmetry research: three MPA studies examined children, but none of the symmetry studies described here do so. However, given the prospect that they tap the same underlying latent trait of integrity, it is plausible to expect the symmetry findings to extend to children. More work including both symmetry and MPA measures would help resolve this issue. This work next describes links between symmetry and another major area of interest in psychology: personality and behaviour.

1.8 Symmetry, Personality and Behaviour

Symmetry then, has robust links to cognitive attributes, though there are outstanding issues with the age ranges used, the typical sample size, and the inconsistently found sex differences. But it seems implausible that such a relationship with intelligence would be found across the lifespan if symmetry was informative purely because it was a byproduct of an evolved preference for symmetry. As such the relationship between symmetry and cognition appears to be caused by both these variables indicating underlying bodily system integrity (though the conclusions remain tentative). It is then plausible to expect symmetry to be associated with many important outcome variables, and symmetry can be used as a tool to assess competing theories describing the fitness relevance of such variables.

This is especially relevant in the context of personality and behaviour. There is an ongoing debate on the causes of individual differences in personality and behaviour (Penke, Denissen, & Miller, 2007). Several arguments have been proposed. With regards to personality, some have suggested that well developed organisms should exhibit specific personality patterns with some traits (such as high extraversion) being consistently beneficial and non-beneficial personality or behaviour resulting from high mutational load which might be indexed by symmetry (Shackelford & Larsen, 1997). Serious mental illness might be a sign of a system wide problem (Weinberg, Jenkins, Marazita, & Maher, 2007). Alternatively the relationship might be indirect; well-built and successful individuals may have less need for cooperation (Zaatari & Trivers, 2007).

Using symmetry, it is possible to test these possibilities. If some personality or behavioural attributes are beneficial, they should correlate with low asymmetry. Those with severe mental illness should exhibit higher asymmetry than controls. If the relationship between symmetry and behaviour is mediated by other characteristics (such as possessing a well-built system overall, or higher intelligence) this is also testable. In practice, relatively little work has been done and much of it tests only a few relevant variables at a time, or does not control for potentially confounding factors (such as age). The discussion here focuses particularly on personality, aggression, cooperation, and mental illness.

Personality traits - Neuroticism (N), Extraversion (E), Openness to Experience (O), Agreeableness (A) and Conscientiousness (C) – have well established links to well being. E is associated with self-reported health (curvilinearly – high E individuals report more symptoms) and high N is associated with poorer health behaviour (Williams, O'Brien, & Colder, 2004). Conscientiousness is related to health and more conscientious individuals live longer (Kern & Friedman, 2008; Kern, Friedman, Martin, Reynolds, & Luong, 2009). This suggests some personality traits may be related to the overall functioning of the organism, either as a consequence of underlying integrity, or as a factor which across the lifespan causes individual differences in integrity as a result of better or worse choices.

Research on attractiveness has suggested there are cross-culturally stable personality characteristics that are highly related to attractiveness (Buss & Shackelford, 2008): if this is correct then some aspects of personality should associate with high underlying bodily system integrity and with symmetry. Such arguments suggest that high symmetry individuals should

exhibit high scores on E, O, A and C, but low scores on N. If such findings consistently appear and can be generalized to the whole population it would have important implications for our understanding of the evolutionary basis of personality as it would confirm that scores on a personality trait are advertising quality and explain individual differences in personality as at least partly arising from underlying differences in bodily system integrity, with some forms of personality being maladaptive or indicating a distressed system.

However, this is not the only possible explanation. Another model suggests that the optimal personality scores are close to the mean score for the population, with high or low scores indicating high mutational load. Since high mutational load would result in a wide variety of deleterious outcomes, it could be measured via symmetry: high asymmetry would be expected to correlate with extreme scores on personality traits (Gangestad, 2010).

Finally, it is possible that balancing selection may lead to a distribution of phenotypes (Penke, et al., 2007). In this scenario, there is a distribution of phenotypes and no net relationship to fitness. In this scenario, if personality traits do not relate to fitness, there should be no association between symmetry and any of the five traits either linearly or curvilinearly, or with the proposed general factor.

Symmetry, then, can be used to assess important theoretical questions in relation to personality and help identify how valid different theoretical explanations for individual differences in personality are. In doing so symmetry research can assess a question important for policy reasons: why personality traits predict health and longevity. However, existing research tends to rely on small, college age samples.

1.8.1 Empirical Findings: Symmetry and Personality

Shackelford and Larsen (1997) examined links between facial asymmetry and a number of personality measures including the Eysenck Personality Questionnaire. The sample size was made up of 101 college undergraduates (mean age approximately 20). High asymmetry was associated with E in women only ($r = .32$) and N in men only ($r = .49$). Given the number of tests involved in the study it is possible these are type 1 errors. Equally, it is not clear why high asymmetry would be associated with high extraversion: given the cross-cultural desirability of traits described briefly earlier, the opposite would be expected (Buss & Shackelford, 2008). On the other hand, other research has suggested high E may associate

with poorer health (Williams, et al., 2004), so such research provides at least some empirical support for the findings that high E may have some negative outcomes.

Subsequent research, however, renders the relationship between symmetry and personality unclear. Fink, Neave, Manning and Grammer (2005) used a measure of facial asymmetry and the NEO-Five Factor Inventory (Costa & McCrae, 1992) to test associations between symmetry and personality. They tested 120 undergraduate participants, of which 50 were male (age $M = 22.5$, $SD = 4.9$) and 70 female (age $M = 22.9$, $SD = 4.3$), and found higher facial asymmetry was significantly associated with lower E ($r = -.21$), higher A ($r = .23$) and O ($r = .30$) with a nonsignificant trend to higher N ($r = .17$). Asymmetrical participants were more introverted, more agreeable and more open to experiences.

Finally, Pound, Penton-Voak and Brown (2007) tested links between facial symmetry and personality as measured by an adjectival rating task of the big five traits with 294 undergraduate participants (146 male and 148 female) aged between 18 and 22. Of the five traits, only extraversion was significantly associated with asymmetry ($r = -.21$); more asymmetrical participants were more introverted. Notably, despite the large sample size and the similarity of both the participants and the methodology, they could not replicate the associations between symmetry and E, A, or O described by Fink et al. Work on MPAs is too limited to clarify the issue. Paulhus and Martin (1986) found that, among 87 undergraduates, those with more MPAs had higher E, but that this was true only for men. It supports the contention that there may be a link between underlying integrity and E but not the direction.

As such, in spite of the fact that research on symmetry and personality may provide considerable information on the underlying causes of individual differences in personality and the fitness consequences of different traits, existing research provides no well established relationships for any of the traits and all rely on college age participants. Use of college age participants means the sample is likely to be of above average intelligence. Changes in the relationship between personality and symmetry over time have not been tested. More research here to assess the prospect that the disagreement stems from type 1 errors (testing five personality traits separately for males and females produces ten separate tests per study) would be helpful, especially if paired with an examination of links between symmetry and intelligence in the same sample where the relationship is more robust. If symmetry associates

with intelligence in such a study, but not with personality, this would provide stronger evidence that the personality traits do not associate with symmetry.

Another important aspect of behaviour connected to symmetry concerns cooperation and aggression. The degree to which symmetrical individuals are cooperative (having higher intelligence and perhaps therefore having more to gain from such ventures) or uncooperative or even aggressive (being 'well built' they have a great likelihood of successful aggression or less need to cooperate with others) is unclear and the use of symmetry in such research may resolve the issue empirically.

1.8.2 Empirical Findings: Symmetry, Aggression and Cooperation

Research on aggression is more problematic due to the ethical constraints involved in measuring such behaviour. However three relevant studies have been conducted. These provide information on symmetry and aggression as well as providing further concern over how age may influence associations between symmetry and other outcome variables across the lifespan.

Furlow, Gangestad and Armijo-Prewitt (1998) examined 229 undergraduates (90 male, 139 females), who were measured for ten bodily symmetry traits. Participants recorded information on the frequency of physical fights in recent history, which were initiated by them, and which were initiated by others. They also completed a measure of aggression, designed to score participants for physical aggression, verbal aggression, anger and hostility. Asymmetrical men fought significantly less ($r = -.25$) and were less likely to initiate aggression ($r = -.49$), whereas for women both these relationships were nonsignificant ($r = -.01$ and $.05$ respectively).

These findings were supported by Manning and Wood (1998). They measured symmetry via five bodily traits, and examined self-reported physical aggression in 90 boys (age $M = 12.6$, $SD = 0.1$) from one Liverpool school. Asymmetrical boys were significantly less physically aggressive. This research, combined with that of Furlow et al., suggests more symmetrical males may be more aggressive across childhood and adult life.

However, the association between asymmetry and aggression may be more complex than a simple linear association. At least some evidence links low intelligence to high aggression (Huesmann, Eron, & Yarmel, 1987) whereas asymmetry has previously been linked to high

intelligence. Subsequent work may explain these findings. Benderlioglu, Sciulli and Nelson (2004) tested the relationship between symmetry and reactive aggression in 100 participants (age $M = 20.1$) of which 51 were male and 49 female) using 11 bodily symmetry traits. Reactive aggression referred to the degree of hostility in responding to intrusive requests. They found that among both males and females high asymmetry was associated with high reactive aggression when provocation was low and chose to respond with hostility when given the opportunity. This trend was reversed when under high provocation. As such, the link between symmetry and aggression is partly situational – rather than being aggressive in all circumstances, low and high symmetry individuals differ in the circumstances likely to generate aggressive behaviour, and what form that behaviour takes. The level of aggression exhibited may be informative of underlying system integrity, and the situation in which aggression manifests may be more important than the level of aggression. The limited amount of parallel work done with MPAs supports this; Waldrop et al. (1968) found that children aged around 2 and a half who had more MPAs were more, rather than less aggressive: the circumstances in which aggression manifests seems to be more important than the level of aggression.

This research can be complemented by examining cooperation. Zaatari and Trivers (2007) tested cooperation an ultimatum game in Jamaica using seven bodily symmetry traits. The ultimatum game involved splitting money with another individual; the participant would choose to accept or reject the offer. Testing 153 participants (age $M = 15.9$, $SD = 1.7$) of which 84 were male and 69 female, symmetrical males made significantly lower offers than asymmetrical males but the relationship was non-significant in women. This supports the idea that symmetrical individuals are in a position to expect better deals and consequently less likely to be cooperative.

In a follow up study, Zaatari, Palestis and Trivers (2009) using a subsample from the study described above (188 participants, of which 106 were male and 82 female, age $M = 18.1$, $SD = 1.8$), tested links between level of offers in an ultimatum game and the symmetry of the receiver. By contrast to the previous study, each participant would view a photo of a young adult before making offers. These individuals had no contact with the participants at any time and were not drawn from the same country. 20 photos were used: 5 were among the most symmetrical males, 5 among the most symmetrical females, 5 among the least symmetrical

males and 5 among the least symmetrical females. There was a small tendency to give more to the symmetrical individuals (Cohen's $d = 0.11$). There was also a significant tendency for participants to report giving larger sums to symmetrical individuals because they were attractive, whereas those who gave more to asymmetrical individuals tended to state the individual appeared to need assistance.

Collectively, these findings present evidence that aggression and cooperation vary between individuals and across different circumstances and that these attributes relate to symmetry. There is little reason to expect a residual preference for symmetry to cause this: the participants in Zaatari et al. (2009) who gave more to the asymmetrical individuals explicitly noted that appeared to be in greater need. Similarly, a difference in laterality does not easily explain the consistent and complex links between symmetry and aggression. This work supports the proposition that symmetry is associated with underlying bodily system integrity, can provide information on the circumstances in which low or high integrity individuals are likely to be aggressive and conversely gain information about aggressive individuals from the circumstances in which they tend to be aggressive.

1.8.3 Empirical Findings: Symmetry and Mental Illness

Such research may be especially productive when applied to maladaptive behaviour or mental illness. Given the associations between symmetry and intelligence and behaviour described here, and the proposition that symmetry indexes bodily system integrity, it is plausible that the incidence rate and severity of mental illness will be increased among those who exhibit higher asymmetry. More than any other area of the literature, MPAs have been studied in connection to the mentally ill. As such this section will discuss symmetry then MPAs with a view to assessing how their relationship with mental illness may be informative of underlying bodily system integrity.

Martin, Manning and Dowrick (1999) tested 102 Liverpool residents (52 male and 50 female) on six symmetry traits. They measured depression via the Beck Depression Inventory (BDI) (Beck & Steer, 1984). Asymmetrical men exhibited more severe depression but the relationship was nonsignificant in women. If symmetry is indicating the well-functioning of the organism, mental illness may be indicative of a system-wide problem.

Most of the work linking symmetry to schizophrenia tested the relationship using dermatoglyphic asymmetry (typically measured by the number of ridges on each hand or finger). Markow and Wandler (1986) tested the level of dermatoglyphic asymmetry in 81 schizophrenics, 14 individuals with schizoaffective disorder, 49 individuals with affective disorder and 69 faculty and staff members at the institution where the research took place (both the latter groups were controls). Schizophrenics exhibited significantly higher asymmetry than the control group.

This finding has subsequently been replicated. Mellor (1992), again using dermatoglyphic asymmetry, tested symmetry in 482 schizophrenics (232 male, 250 female). As compared to non-schizophrenic controls, the schizophrenics exhibited significantly higher asymmetry. Reilly et al. (2001), tested 30 patients (19 male, 11 female, age $M = 27.9$, $SD = 8.3$) who were schizophrenics and matched them with controls. The schizophrenics exhibited significantly higher asymmetry than the controls.

This suggests that high levels of asymmetry are associated with more frequent or more severe mental illnesses. Given the proposal that such conditions may originate in early childhood disorders or reflect underlying bodily status, parallel markers to symmetry may also relate to mental illness. The evidence linking MPAs to mental illness is robust. Recent meta-analyses of links between MPAs and schizophrenia (Weinberg, et al., 2007) and autism (Ozgen, Hop, Hox, Beemer, & van Engeland, 2010) have indicated large effect sizes (Cohen's d of 1.13 and 0.84 respectively) with those exhibiting the conditions having many more MPAs than controls.

As in the case of symmetry, the specific body part is in theory unimportant; rather a high number of MPAs is indicative of a serious underlying problem. As noted previously, symmetry and MPAs tend not to be measured simultaneously (especially in the very recent literature) but doing so may provide a better picture of the participant's underlying bodily system integrity. The fact that symmetry (and MPAs) is linked to mental illness is extremely important. Symmetry may be useful as a diagnostic tool with high asymmetry indicating a greater likelihood of an existing or future problem. Given the noted tendency for symmetry to vary across the lifespan, longitudinal work examining symmetry in youth and across the lifespan, paired with an evaluation of mental health, would provide information on the directionality of the relationship and may be useful in planning health interventions.

Mental illness links behavioural and physical problems together. This review will now discuss the evidence linking symmetry to physical health problems and well being.

1.9 Symmetry, Attractiveness, Sexual Behaviour, Fertility and Health

This work has demonstrated links between symmetry and age, cognitive ability, and at least some aspects of behaviour. The evidence broadly supports the proposition that symmetry is measuring some form of underlying well being. The term system integrity has previously been used here, and it is in the context of health that an especially promising use of symmetry in research may be found. Gale, Batty, Cooper and Deary (2009) argued that the utility of system integrity in understanding life-course development hinges on the availability of markers of the construct. Symmetry appears to be one such marker, and as such can provide considerable utility in all domains. However, as Gale et al. note, any putative marker must relate to cognitive ability and health. The former is well demonstrated. This review will now discuss the latter.

Research into symmetry and health is broad-based. Much of the early work derived from evolutionary theory which regarded honest signals of fitness to be important when selecting a mate (Thornhill & Gangestad, 1994). Following this, signals indicating underlying system integrity should be regarded as attractive as they indicate health and fertility. Symmetry, as an indicator of this integrity, would then be expected to associate with attractiveness as well as health. This section will discuss links between symmetry and attractiveness, sexual behaviour, fertility, then move on to the literature that has modelled specific health outcomes.

Gangestad, Thornhill and Yeo (1994) argued that the cross-cultural nature of attractiveness derives from evolutionary mechanisms that aid the selection of mates resistant to illness. Using seven bodily symmetry traits, they tested 72 undergraduates (age $M = 23.2$), of which 35 were female and 37 were male. Eight raters scored the participants for attractiveness on a 10 point scale, 1 indicating least attractive, 10 indicating most attractive. After controlling for age and sex, higher asymmetry significantly predicted lower attractiveness ($r = -.25$).

Follow up work has typically been conducted in broadly similar sample types. Perrett et al. (1999) used images of 30 individuals (equal numbers male and female, all aged between 20 and 30 years) to test the relationship between symmetry and attractiveness. Rather than comparing different individuals, faces were visually manipulated so each individual had a

high and low symmetry image of themselves. The images were then presented to 49 raters (12 male, 37 female, aged 18 to 22 years). Raters preferred the more symmetrical image significantly more often. Such findings are important because they demonstrate the link between symmetry and attractiveness is not solely due to broader differences on the part of more or less symmetrical individuals: symmetry itself is the trait driving (some of) attractiveness.

1.9.1 Empirical Findings: Symmetry, Attractiveness and Sexual Behaviour

Gangestad, Merriman and Thompson (2010) identified a link between symmetry and attractiveness in 98 males (age $M = 20.1$, $SD = 2.9$). Ten bodily asymmetry traits were measured. Five raters scored the participants on a 10-point scale. High asymmetry was associated with significantly lower attractiveness ($r = -.22$), and the researchers extended the analysis to consider explicit measures of health which will be discussed later.

This evidence suggests that symmetry is an honest signal of fitness and consequently linked to health. If correct such findings could be supported by evidence from sexual behaviour. While limited in number, existing studies tend to support this proposition. Thornhill and Gangestad (1994) tested 122 undergraduates of which 60 were male (age $M = 24.1$, $SD = 5.3$) and 62 female (age $M = 24.0$, $SD = 5.8$), using seven asymmetry traits. Participants reported data on their age at first sexual encounter and their lifetime number of sexual partners. Higher asymmetry was significantly negatively associated with the number of lifetime partners for men ($r = -.32$) and women ($r = -.36$) respectively.

This research has been extended to examine other areas of sexual behaviour. Gangestad and Thornhill (1997) tested 203 heterosexual couples (male age $M = 21.1$, $SD = 3.6$, female age $M = 20.0$, $SD = 3.2$), all in a relationship of longer than one month in duration. Participants reported whether they had engaged in extrapair sex in the current relationship (that is, whether they had had sex with someone other than their partner, and if so with how many individuals) as well as the lifetime occurrence of extrapair sex. They were also asked whether they had had sex with someone they knew to be in a relationship with someone else. Asymmetry was measured on seven bodily traits. High asymmetry significantly predicted a lower number of extrapair partners in that relationship, a lower number of extrapair

encounters in total, and less likelihood of sex with a partner in another relationship for males. For females all relationships were nonsignificant.

Symmetry is related to attractiveness and sexual activity. It is also related to fertility in both men and women. Jasienska, Lipson, Ellison, Thune and Ziomkiewicz (2006) tested 171 Polish women aged between 24 and 36 on one asymmetry trait. Asymmetrical women had lower potential fertility: they scored negatively on multiple measures that predicted likelihood of contraception.

Manning, Scutt and Lewis-Jones (1998) examined 61 men (age $M = 33.5$, $SD = 0.8$) undergoing infertility treatment. Using 4 asymmetry measures, they identified a trend for more asymmetrical men to have significantly lower total sperm number, lower sperm speed, and lower sperm migration rate.

1.9.2 Empirical Findings: Symmetry and Health

As such, the evidence linking symmetry to attractiveness, sexual behaviour, and fertility suggests plausible links to health. They also suggest symmetry has a direct relationship to underlying system integrity rather than simply being a by product of an evolutionary preference (van Dongen, 2011). Health in different periods of life, and for different conditions, must be discussed.

The first issue is symmetry of the foetus. This is difficult to measure but some studies have attempted to evaluate foetal symmetry post-mortem. Van Dongen, Wijnaendts, Ten Broek and Galis (2009) examined 643 deceased fetuses (310 male, 273 female) for asymmetry of seven bodily traits. Asymmetry increased with the severity of the disorder the foetus experienced, but maternal problems did not predict asymmetry.

Livshits et al. (1988) examined the relationship between asymmetry and preterm birth. When comparing 113 preterm infants to 103 term infants, they found that preterm infants exhibited significantly higher asymmetry compared to term infants.

Both foetal and neonatal health effects are associated with symmetry. Symmetry in newborns also appears to be associated with status of the parent, though in practice this has been measured only as status of the mother. Kieser, Groeneveld and Da Silva (1997) examined the interaction of obesity and smoking. They tested 111 obese smokers, 114 obese non-smokers,

104 non-obese smokers, and 111 non-obese non-smokers. Offspring of the mothers were all aged between 10 and 16. The researchers measured asymmetry via two traits, and found that mothers who were obese and/or smokers had more asymmetrical children. Childhood symmetry can be reduced by parental activity, though it is not known from such research whether the effects are lifelong or modifiable as a result of later events.

Symmetry is also linked to adult health, though the measures used tend to be diverse with little replication of specific illnesses. Waynforth (1998) examined 56 men living in rural Belize using 8 bodily asymmetry measures. Asymmetrical men experienced more serious illnesses ($r = .31$) and had fewer offspring.

Research conducted in environments with access to modern medical care has produced somewhat equivocal results. Discussed earlier in the context of attractiveness, Gangestad et al. (2010) found high asymmetry was positively associated with oxidative stress ($r = .26$), which is itself a cause of mutation and bodily deterioration. Greater parasite load is associated with higher asymmetry in humans across many studies (Møller, 2006), though most of these are in nonhumans.

Rhodes et al. (2001) scored 316 participants (155 male, 161 female) aged around 17 on facial asymmetry. A composite health score including indicators such as level of infectious condition and their severity did not associate significantly with asymmetry despite a larger sample size than those described previously.

Milne et al. (2003) tested symmetry via six traits in 965 participants (490 male, 475 female) aged around 26. Some links between asymmetry existed, but were not consistent: high asymmetry was associated with a greater number of medical conditions but not blood pressure, fitness, BMI, or degree of periodontal disease. Considerably larger than any other study described here, this research had the capacity to identify very small effect sizes.

The tendency for findings to be inconsistent, or extremely variable in effect size, was an issue highlighted in the meta-analysis by Van Dongen and Gangestad (2011) discussed previously. Effect sizes remain heterogeneous, and the cause of this is unclear. Milne et al. suggested several possibilities specifically in relation to humans: high quality medical care may obscure the relationship between symmetry and health except for the especially ill or unhealthy, or

links between symmetry and health may be age dependent and as such emerge with greater consistency later in life.

There is, then, evidence that some health effects are linked to symmetry. Such findings have been demonstrated more clearly in nonhumans (Knierim, et al., 2007) but relationships are present in humans as well. The magnitude of the effect sizes varies considerably and there are few replications of individual health measures such as oxidative stress which might help clarify the issue.

1.10 Symmetry and Early life Circumstances

Understanding the relative importance of early versus later life circumstances is of considerable policy importance. For example, early life socioeconomic status (SES) whether assessed by parental income, education, or prestige, is associated with the health and longevity of the offspring (Doyle, Harmon, Heckman, & Tremblay, 2009). There is evidence that the early environment plays a distinctive role in lifelong health and wellbeing as dysregulation of basic developmental processes including cellular division, growth, and hormonal signalling are modified during the prenatal and early period in response to circumstances. Life history strategy is then programmed based on the received information; Barker (1995) identified that in some circumstances, poor early life circumstances led to poor outcomes regardless of whether midlife circumstances were good or bad. The individuals had adapted to grow and reproduce rapidly in anticipation of a poor environment.

Symmetry can be of use in investigating this topic. Symmetry as an outcome measure for indicating underlying system integrity can be measured at any age (Gregory Livshits, et al., 1998) and consequently can be used to test outcomes that might otherwise be difficult to measure due to early or midlife well being having different indicators. Parental and personal SES may not be directly comparable for instance, as a result of changing demographics. Furthermore, such research would provide considerable insight into the utility of symmetry by examining whether high asymmetry adults exhibiting poor outcomes, as described elsewhere in this review, have always exhibited high asymmetry or whether this has been acquired at some point during the middle of the lifecourse. If high asymmetry is a constant throughout an individual's life, this would argue that early developmental or possibly genetic factors led to the asymmetry and the poorer outcomes. On the other hand, if high asymmetry

as a result of poor childhood circumstances could be reversed in midlife – similar to the childhood trend for symmetry to increase rather than decrease (Manning, Koukourakis, & Brodie, 1997) – this would suggest an improvement in circumstance could improve symmetry and therefore potentially reduce the likelihood of the individual encountering these adverse outcomes. Detailed research might identify the optimum time for such interventions.

1.10.1 Empirical Findings: Symmetry and Socioeconomic Status

SES, which is important for a variety of health outcomes (Marmot, 2010), has only rarely been tested in symmetry research. As is the case with age, some studies using primarily college age samples, have tested SES without focusing on it as a main analysis, but college age samples may exhibit range restriction for SES as they do for age (Thornhill & Gangestad, 1994). Furlow, Gangestad and Armijo-Prewitt (1998), for instance, measured participant SES in a college undergraduate sample (described previously) but did not report correlations between symmetry and SES, instead using it as a control in their main analysis.

However, some research has been done in environments where there are substantial differences in early life circumstances according to area of residence. Özener and Fink (2010) examined facial symmetry in 503 Turkish students (aged around 17 years). 133 males and 117 females were recruited from a slum, and 131 males and 122 females were recruited from a wealthy area. Using facial asymmetry, they identified a trend for the slum dwellers to exhibit significantly higher asymmetry than the wealthy area dwellers. Subsequent work examining 320 male participants from the same geographical area, using eight symmetry measures of the body, found those with higher asymmetry had a shorter final body height (Özener & Ertuğrul, 2011). Taken together, the two studies suggest that adverse early circumstances as measured by SES cause measurable differences in symmetry at the point where individuals enter the reproductive phase. As such, given the tendency noted earlier for symmetry to be influenced by parental behaviour (Kieser, et al., 1997) and for asymmetry to increase during the growth spurt (Manning, et al., 1997) it is plausible that early life SES has an effect on the organism until at least the start of the reproductive phase. Whether this effect is permanent is at present unknown.

Research on other childhood circumstances is extremely sparse. Flinn, Leone and Quinlan (1999) tested 238 children (age $M = 10.6$) and examined whether symmetry, as measured by

7 traits, was higher in those living with a stepfamily. As stepchildren are not genetically related to one of the adults, they are typically thought of as a cost to that adult as aid given to them is not beneficial and may reduce investment available to future genetic offspring with the stepchild's parent (Daly & Wilson, 1996). However, while the stepchildren exhibited lower height and body weight, they exhibited lower asymmetry. This finding is in the opposite direction that which was predicted, but no follow up work has examined the issue; the authors discuss the possibility that this is related to timing of growth spurts (see e.g. Manning et al. 1997) but this has not been empirically confirmed. Symmetry may be related to family circumstances but the existing evidence is too limited to draw firm conclusions.

There is considerable evidence linking symmetry to important indicators of well being. This review will briefly examine the major weaknesses of the field before discussing the present studies.

1.11 Limitations in existing work

Despite the considerably body of evidence linking symmetry to a variety of important outcome traits, there are significant limitations in existing work. Some of these issues reflect problems discussed in section 1.2 of this review and will be discussed now with reference to the body of literature examined. These problems include low sample sizes, a lack of a canonical set of symmetry measures, a lack of controlling for additional important covariates (notably age) and a tendency not to account for sex differences.

1.11.1 Sample Size

The issue of sample size is highly problematic. Van Dongen and Gangestad (2011) suggest samples of under 100 should be avoided, and samples of 350 should be used to ensure adequate power (80% chance to detect effect sizes of those typically found i.e. $r = .15$). Of the symmetry studies described here in relation to their empirical findings, excluding reviews, 12 have a sample size of under 100, and only 7 have sample sizes over 350 (out of a total of 37 studies specifically linking symmetry to outcome measures of interest to this review). There are not enough large powerful studies examining what are expected to be small effects, and this makes it very difficult to clarify which findings are genuine and which are due to low power.

1.11.2 Diversity of Symmetry Measures and Methods

There is also a great deal of diversity in the usage of symmetry traits. The work described here uses all the methods described in section 1.2. However there are few attempts to verify the different traits used against each other. So, there is little tendency to use facial and bodily symmetry, or measure bodily symmetry and dermatoglyphic symmetry in a single study. Even more problematically, there is a tendency for different research groups and those researching different topics to use one particular method almost exclusively. For example four of the studies relating to schizophrenia used dermatoglyphic asymmetry, whereas none of the studies investigating personality traits did so. This is problematic as without knowing the relative utility of different symmetry traits it is possible some findings occur because the traits are especially good or bad at indicating underlying system integrity. While it is typical to assume that traits are interchangeable, improvements in design could test this empirically. It is useful for any one research group to use established methods for which the researchers are well trained and have reliably used in the past, but this makes it more problematic to ensure equivalence across different areas of symmetry research.

1.11.3 Failure to Control for Potential Confounds

The lack of attention to important covariates is partly a byproduct of the typical sample types used. College age students generally provide limited information. Several examples of large cohorts have been described here (Kobyliansky & Livshits, 1989; Milne, et al., 2003), and these provided the opportunity to investigate symmetry in depth in relation to a variety of important outcome measures in a single sample. Such samples therefore provide multiple advantages over college student samples, and where symmetry research can be linked to these conveniently there is the opportunity for a great deal of productive research in a large sample for relatively little investment of time and resources. The reliance on college age participants makes understanding symmetry across the lifecourse problematic. Of the symmetry studies described here, 9 cover children (under 18) and of the remaining 28, 18 have sample means under the age of 30. Only 1 study has a sample mean of over 50.

1.11.4 Lack of Certainty over Sex Differences

Sex differences are often noted, but inconsistent. While females sometimes exhibit significantly higher asymmetry than males (Bates, 2007) this is not always true (Özener &

Fink, 2010) and the causes of this inconsistency are not known. Based on theoretical arguments pertaining to sexual selection theory, some researchers have suggested there should be stronger links between symmetry and important outcome measures for males (Gangestad, et al., 2010). However, such reports are also inconsistent. Some research found significant associations between aggression and symmetry in men only (Furlow, et al., 1998) whereas others found no differences between the sexes (Benderlioglu, et al., 2004). With respects to intelligence, some researchers have found significant associations between symmetry and intelligence in men only (Rahman, et al., 2004) whereas others have found associations in both sexes (Luxen & Buunk, 2006). As the meta-analysis of symmetry intelligence measures notes, both sexes should be tested to help understand the nature of the relationship (Banks, et al., 2010), but in practice few studies have sufficient power, especially if the effect sizes are expected to be smaller among women than men.

This concludes the review of the empirical evidence and the discussion of the outstanding issues that need to be resolved to improve symmetry research. The next section briefly discusses the theoretical explanations for links between symmetry and the outcome measures discussed in the preceding five sections.

1.12 Conclusion: The Usefulness of Symmetry Research

As discussed in section 1.3 there are two major explanations for the links between symmetry and the outcome measures discussed in sections 1.6-1.10. Firstly, symmetry might indicate underlying well-being, and so provide a measure of the overall state of the organism (van Valen, 1962). Secondly, symmetry might be indicative of lateralization or an evolved preference for symmetry (van Dongen, 2011). While the work described here cannot conclusively resolve the issue, it is notable that symmetry is correlated with other indicators of underlying integrity which would not be affected by lateralization in the form of MPAs (Weinstein, et al., 1999). Given the breadth of research documenting the trend for symmetry to be linked to adverse outcomes, and especially noting the tendency for symmetry to fluctuate up and down over time (Manning, et al., 1997) it seems plausible that symmetry indexes a form of underlying integrity.

As such, symmetry can be useful in essentially three ways. Firstly, it may provide information of underlying stability, which in turn provides opportunities to explore the fitness

relevance of traits and the evolutionary mechanisms of characteristics that associate with symmetry. Secondly, it can assist efforts to identify a latent trait of bodily integrity that may account for individual differences across multiple outcome measures. Lastly, it can help understand the relative importance of different life stages to the well being and health of the organism, and consequently provide a means of evaluating relative wellbeing throughout the lifespan. The samples and methods to be used in the present studies will now be discussed, followed by a review of how each sample will contribute to answering the outstanding questions discussed above.

Chapter 2: Overview of Samples and Methods

This section gives a general overview of the four samples used in the present work. It also provides an account of the evolution of the method of measuring asymmetry from the start to the end of the thesis and how this has improved upon the methods used by others. The chapter-specific measures not related to symmetry are not described here in detail: they are covered in the relevant empirical chapters.

2.1 Description of samples used in the empirical work

Each of the four samples has been used in a number of studies beyond those described in this thesis. Here only the key elements are described. Due to incomplete assessment on individual phenotypes, the total sample sizes reported here are somewhat higher than those reported for the variables of interest in each chapter.

2.2 The Lothian Birth Cohort 1921

The Lothian Birth Cohort 1921 (LBC1921) are surviving participants of the Scottish Mental Survey in 1932. They were recruited between 1999 and 2001 while in the Edinburgh area (Deary, Whiteman, Starr, Whalley, & Fox, 2004). Originally 550 participants were involved, with testing phases occurring from age 79 onwards with the most recent data described in this study occurring at age 87 (Gow et al., 2011). Primarily designed to examine lifespan cognitive change and factors contributing to it, all participants – along with all other residents of that age in the Lothian area – had completed a well-validated test of cognitive ability in the form of the Moray House Test at age 11. Unusually, this meant the sample possessed a measure of childhood intelligence rather than having to estimate it from performance in middle or old age. This cognitive test was re-administered in old age, along with other measures of cognitive ability. Information on health, well-being, socioeconomic status (SES) and family status were collected, sometimes at each wave. Wave 1 was conducted at around age 79 (M age = 79.2, SD = 0.6), wave 2 at around age 83 (M age = 83.4, SD = 0.5) and wave 3 at around age 87 (M age = 86.7, SD = 0.4). This was advantageous in several respects. Measures of early life – especially SES – were available and described a period of time much

further back from the symmetry testing phase than was typical in most symmetry studies. For the purposes of evaluating SES, for example, the impact of SES on symmetry was measured over 70 years after the childhood circumstances recalled by the participants. The intensively studied nature of the sample provided opportunities to control for important background characteristics that are typically under-examined in symmetry research. The symmetry measures themselves were unusually thorough: asymmetry was measured in the face at age 83 and in the body at age 87, allowing for a broad range of asymmetry measures in many different areas of the body. These measures are described in more detail later in this chapter. The sample is much older than is typical for symmetry research: only one study in the introduction included research in a sample with a mean age over 50 and it was conducted on this sample (Penke, et al., 2009). In total 216 participants contributed to some form of symmetry measure. These are described in more detail in the relevant empirical chapters. A full list of publications from the LBC1921 can be found on the study website (www.lothianbirthcohort.ed.ac.uk).

2.3 The Science Festival Sample

The Edinburgh science festival is an annual event designed to engage the public – especially children – with all areas of science. The participants described here were child visitors who attended the Medical Research Council (MRC) event at Easter in 2009 or 2010 aged between 4 and 15 years. The mean age was 9.4 ($SD = 2.3$), though see chapters 4 and 6 for values for each analysis. The festival as a whole required an entry fee and the MRC event was located in an easily accessible city centre building. Parental consent was sought for participation of each child. Where this could not be obtained, no data were recorded. The event was structured as an educational experience exploring links between the mind and the body. Each child completed a series of linked exercises. For both 2009 and 2010 this included measures of Reaction Times (RTs) and symmetry. In 2009 only data on the SES of the participants was recorded. In 2010 only data on grip strength and laterality was recorded. Some of this research – specifically the part focusing on RTs – has been described elsewhere (Dykiert, Der, Starr, & Deary, submitted). A total of 896 participants contributed usable symmetry data, which was measured digitally in the hands. This sample represents one of the largest child samples available to date and exceeds the sample size of Wilson and Manning (1996).

2.4 The Orkney Complex Disease Study

The Orkney Complex Disease Study (ORCADES) is a cross-sectional family based study of residents in the Scottish island group Orkney. Data collection began in 2005 and eventually tested 2080 participants in total. These individuals were tested on over 300 health-related phenotypes and environmental exposures were recorded in each case. The measures included information relating to disease, SES, cognitive ability, and family status among others. In total 1200 participants were scored for asymmetry of the bones. These were the humerus, ulna, radius, femur, fibula and tibia The ORCADES has produced a large number of publications: for further details see McQuillan et al. (2008).

2.5 The Berlin Sample

The Berlin Sample (BS) was used in only one study. It was used here to expand the sample size of one empirical chapter (chapter 8) and is included here for completeness. Full details of this sample can be found in Penke and Asendorpf (2008). This sample was initially recruited for a study on personality and relationships, and included measures of relationship status, personality, and symmetry. Bodily asymmetry was measured via digital callipers. In total, 207 participants contributed usable asymmetry measures.

2.6 The Measurement of Asymmetry across the Four Samples

All asymmetry measurements used are described both here and in the relevant empirical chapter. The goal here is to describe the evolution of methodology over the course of the thesis. The work is, therefore, described chronologically rather than according to the order of chapters. The next chapter describes which of these methods were used in which section.

2.7 Pre-existing Asymmetry Measures in the LBC1921

2.7.1 Digital Measurement of Facial Asymmetry in the LBC1921

Facial asymmetry was recorded at age 83. Facial photographs were taken for each participant in wave 2 of the LBC1921 (M age = 83.4 SD = 0.5) and is described in detail elsewhere (Penke, et al., 2009). They were used to calculate Horizontal Facial Asymmetry (HFA) and Total Facial Asymmetry (TFA). HFA, the most common and best-validated measure for facial asymmetry in the existing literature (Grammer & Thornhill, 1994) includes only horizontal asymmetries of the face. TFA, on the other hand, also includes additional non-horizontal indicators. The former is better validated, while the latter is more comprehensive. The procedure is based on methods described in the introduction (Simmons, et al., 2004).

Facial photographs were taken under consistent lighting. Shadows can cause errors when attempting to estimate landmark sizes and locations, so consistent lighting is important for accuracy. Participants were instructed to hold a neutral expression during photography. In total, 91 of 314 images were discarded as unsuitable due to inconsistent lighting, non-neutral expression, or obscured landmarks. The remaining 223 images were rotated so the lips were on a horizontal plane. A central midline was drawn through the centre of the face, and distances between landmarks and the midline – the edge of the lips for example – measured. Greater differences in distance between the left landmark and the midline, and the right landmark and the midline, indicated higher asymmetry.

2.7.2 Facial Asymmetry Outcome Measure

All facial traits exhibited high directional asymmetry (DA). A principal components analysis produced one component that reflected DA, and a second component reflecting asymmetry. The second formed the outcome variable of asymmetry described in the present work.

2.7.3 Physical Measurement of Bodily Asymmetry in the LBC1921

Bodily asymmetry was recorded at age 87 using digital callipers accurate to 0.1 mm. Each trait on the left and right sides were measured three times each. Digits 2 to 5 (i.e. all excluding the thumb) were measured along with ear height and width, wrist circumference, elbow circumference and ankle circumference. In total 186 participants were measured on at least one symmetry variable (87 male, 99 female). A digital hand scan was also recorded (see fig 2.1 for three individual examples).

Fig 2.1: Three digital hand scans



Note: Each handscan is of a different participant. The participant on the right exhibits a high level of curvature in the fifth digit that may make a straight line measurement of length inaccurate.

Fig. 2.1 shows that at least some participants exhibited high levels of curvature in the fifth digit which rendered measurements inaccurate. As callipers can only record straight lines, it was not possible to accurately measure these digits and given the inaccuracy, it was possible curvature was inflating the asymmetry score. The next section describes attempts to measure asymmetry in the LBC1921 hand scans more accurately, and how the problem of curvature was accounted for. The next section also marks the first measurement work conducted as part of this thesis.

2.7.4 Digital Measurement of Hand Asymmetry in the LBC1921

Digital measurement via image appears to be more reliable than measurement via callipers (Kemper & Schwerdtfeger, 2009). A full discussion of this can be found in chapter 1, section 1.2. Differences between the programs used to measure digital images have not previously been discussed: the advantages and disadvantages of each technique used in the thesis will now be discussed, along with the exact procedure used for each.

The digital measurement of the hands in the LBC 1921 used Adobe Photoshop (available at www.adobe.com). This program is a commercially available image editing and analysis tool.

Handscans – taken at age 87 along with the calliper measurements – were scored for asymmetry. Images with missing or obscured digits were excluded. The length and width of digits 2-5 (i.e. excluding the thumb) were measured. Digit length was measured as the distance from the base of the digit to the tip. Digit width was measured as the distance across the upper finger crease. While all digits exhibited some degree of curvature, this was most problematic in digit 5 (see fig. 2.1). Research examining curvature in detail is described in chapter 6. The lengths of digits 2-4 were measured via a single straight line from base to tip. The length of digit 5 was measured via three separate lines: one for each segment of the finger. This meant that the length of the digit was not influenced by the curvature of the digit. See fig. 2.2 for an example of this. The curvature of the fifth digit was recorded during measurement, and formed the outcome measure for the Minor Physical Anomaly (MPA) described in chapter 7.

Note that due to the nature of scanners – which are very high in resolution but take approximately 15-30 seconds to complete a scan depending on the scanner model and resolution – movement during scanning would create an unusable image. The image would be blurry, or smeared. In all cases where movement during scanning produced a blurred or smeared image (even if only partially) the image would be discarded. This was first done during the scoring of the LBC 1921 hand scans but was repeated for the SFS.

Fig. 2.2: Hand Asymmetry



Note: Digit 5 (the little finger) is measured by three separate connected lines. This participant exhibits very low curvature of the fifth digit.

High resolution digital scanning allowed for a much higher level of accuracy than when using digital callipers. Fig. 2.3 shows a high zoom image of the tip of digit 3 from the previous figure. The very light colouring above the black line is the finger nail.

Fig. 2.3: High zoom image of finger tip



Note: Black line follows path of the initial symmetry measurement.

This degree of accuracy represents a considerable improvement on calliper measurement. All distances were recorded as number of pixels and entered manually into a spreadsheet.

Reliability was assessed by measuring a subset of 25 images twice and calculating the intraclass correlation coefficient (ICC type 3) between the two measurement occasions ($r = .999$). Note that the reporting style for ICC in asymmetry research may at times deviate from that in other fields: see e.g. Gangestad and Thornhill (1997) for an example of its use in asymmetry work and Shrout and Fleiss (1979) for a general overview of its reporting style elsewhere. The very high level of detail observable in the images allowed for a high level of reliability. Using this method, on average 9 participants could be scored per hour.

2.7.5 Limitations of digital measurement in the LBC1921

While this method provided a high level of accuracy in measurement, it exhibited several limitations. Firstly, and most importantly, measurements could be recorded numerically, but not visually. That is, it was not possible to save a path measuring the length or width of a digit for later review. Only the numerical distances could be recorded. This meant it was not possible to evaluate measurement accuracy at a glance – the symmetry measures themselves had to be evaluated and if judged erroneous, the scan needed to be re-measured entirely. This led to a potential problem in that errors could only be evaluated numerically once the image was closed. This in turn tended to leave very high errors detectable (asymmetry scores above 2% are unusual) but not very low errors (which would be better identified visually, by a digit being clearly poorly measured). Secondly, given that the output had to be typed into a spreadsheet, the measurer was aware of the scores as they were input. Very high numbers,

being implausible, may be noticed and corrected at a higher rate than very low numbers that were also errors. High and low score errors would be expected to occur just as frequently (as the error is random) but low errors would not stand out so clearly. Some authors have tried to address this by having a separate measurer and recorder and instructing the measurer to forget the scores upon stating them as best they are able (Gangestad, et al., 2010) but a method in which measurers were genuinely blind to the scores until after the measurement phase was completed would be preferable. Thirdly, there is a considerable practical concern regarding errors when inputting a lot of data. The high accuracy of the procedure meant each score was typically calculated as a five digit number. Digits 2-4 gave 6 measures (length and width for each) while digit 5 gave 4 measures (1 width, 3 length measures reflecting the three segments of that digit). At 10 scores per participant, and five digits per score, 100 participants required 5000 key inputs. While all data was repeatedly checked and screened for error, an automated input system would greatly reduce the time necessary to check scores and ensure they were error free. Increased automation and speed are important where sample sizes need to be high.

2.7.6 Outcome Measure for bodily asymmetry in the LBC1921

The outcome measure for bodily asymmetry in the LBC1921 combined the physical measures described above with the digital measures. The calliper measurements of the hands were not used. This left five physically measured traits and eight digitally measured symmetry traits.

2.8 Asymmetry in the SFS

2.8.1 Digital Measurement of Hand Asymmetry in the SFS

As discussed previously (Knierim, et al., 2007), while many measurements from multiple areas of the body are ideal, this makes acquisition of large numbers of participants problematic. Digital measurement, however, is advantageous in that the participant needs to be present only for the recording of the image, not the measurement. For the work surrounding the science festival the method of digitally scanning the hands was reused for

this practical reason. All symmetry measures in the festival sample were therefore derived from the hands.

Measurement of asymmetry was the same as for the LBC1921 sample described above, except that the fifth digit was measured by a single score as the sample did not exhibit high curvature. However, a new program was used to try and address some of the outstanding methodological problems such as the need to type large volumes of text which is an error prone process and slowed the rate of work. Autometric is a program designed specifically for symmetry and 2d:4d research (DeBruine, 2004) and has previously been used in the assessment of digital images (Kemper & Schwerdtfeger, 2009). The interface can be seen in fig. 2.4.

Fig. 2.4: Autometric Interface



Note: the four paths have been dragged onto the landmarks. Given the software limitations, a separate recording would be needed to measure the widths. The lengths of the measurements are shown in the right hand panel. The 'record' button exports the scores to a text file. Note:

image is of an adult due to ethical concerns of publishing images of a child. The process for measuring children is identical.

This program had several advantages. Rather than recording images individually, it was possible to prepare a ‘batch’ of images to be measured in one sitting. So, a group of 50 images could be included in a batch and rather than opening and closing them individually, each one would open automatically when the ‘record’ button was selected. The scores were recorded automatically and sent to a text file, which meant that typographic errors could not occur and the eventual file could be exported directly into a spreadsheet for analysis. Combined, this method allowed for images to be completed in considerably less time than for the LBC1921 sample. Reliability was assessed in two ways. Firstly, three pairs of images – that is, participants who had their hands scanned twice in slightly different postures – were measured. The ICC (type 3) for the three pairs were .993, .989 and .991 respectively. As in the LBC1921, a subset of 25 images were measured twice and the ICC between the two sets of measurements of the same images was high ($r = .997$). Around 14 participants could be scored per hour with this method.

2.8.2 Limitations of Autometric

While an improvement, the method still possessed limitations. As can be seen in fig. 2.4, the distances in pixels were visible to the measurer. As in the LBC1921 sample, this meant it was possible for the measurer to evaluate symmetry numerically – however inadvertently – and screen out unusual scores based on numbers rather than visible error in the path measurement. Again, while efforts were made to check all scores, a method where the scores were unknown until after measurement would be preferable. The method also had disadvantages compared to Photoshop. It was not possible to test curvature, though this was in practice less of a priority in this sample as the young participants did not appear to exhibit curvature to a degree where the symmetry scores would be invalid. A maximum of four measures could be taken at a time, necessitating two measuring periods for each group of images (once for length, once for width). Despite this, the program was useful overall.

2.8.3 Outcome Measure of asymmetry in the SFS

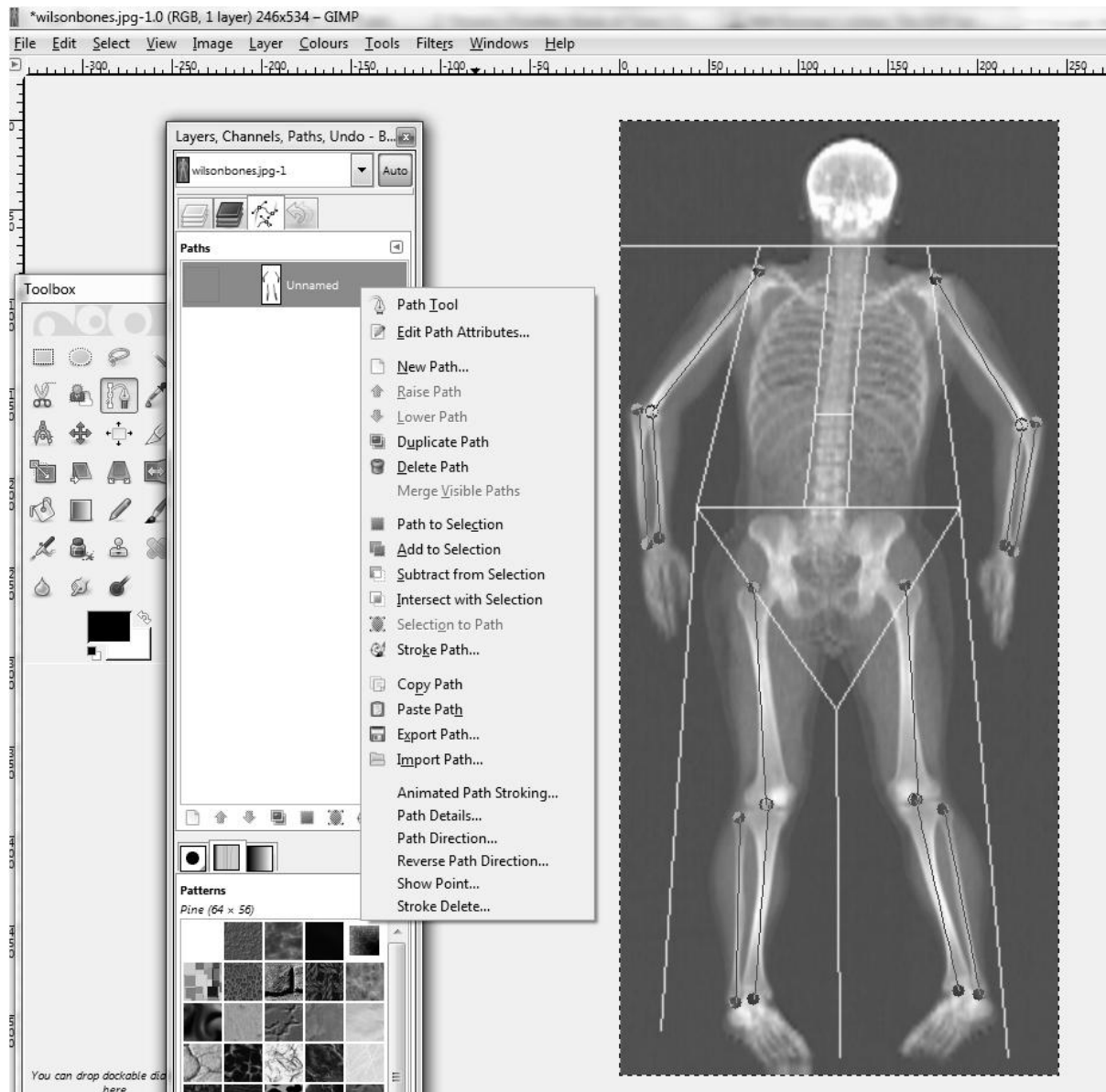
The eight individual measures of asymmetry were combined into a single mean asymmetry score. This was used in all analyses described in the present work. Due to methodological differences in some other aspects of this sample, in some cases a combined score comprising all the 2009 and 2010 participants is presented, and in some cases a separate asymmetry score for each year is presented. See chapters 4 and 7 for more details.

2.9 Orkney Complex Disease Study

2.9.1 Digital Measurement of Bone Asymmetry in the ORCADES

The ORCADES sample, unlike both the prior samples, did not measure symmetry of the hands. Instead, bone symmetry was measured. Bone mass density (BMD) was measured at the lumbar spine, hip, and whole body using a dual energy X-ray absorptiometry (DXA) densitometer (QDR 4500, Hologic Inc., Waltham, MA). As posture was standardized for all participants, it was possible to measure the asymmetry of some of the major bones despite this not being the original purpose of the bone scans. Asymmetry was measured across, initially, six bones on each side of the body: the humerus, ulna, radius, femur, fibula and tibia. Subsequently some of these traits were identified as exhibiting significant DA and were dropped from final analysis: see chapter 5 for full details. An example is provided in fig. 2.5.

Fig. 2.5: Asymmetry of the bones



Note: Lines are drawn across the length of the humerus, ulna, radius, femur, fibula and tibia. The paths can be seen reproduced in the image box under the 'layers, channels, paths' box. The open menu shows the 'export' and 'import' path options which can be used to save the paths numerically or import new paths to superimpose over existing paths for comparison. This bone scan is from a member of the study team, not a participant.

Bearing in mind the drawbacks of Photoshop and Autometric, this research was conducted with GIMP (available at www.GIMP.org). Broadly similar in functionality to Photoshop, this program had several advantages over prior methodology. Importantly, GIMP was used to

measure paths between sites on an image. This path was separate from the original image and could be exported directly containing numerical information including size of all measured paths. Via this method, it was possible to export a full list of items without the measurer being aware of the scores. Consequently, the measurer was obliged to evaluate errors visually rather than by score, and avoided a problem present in both Photoshop and Autometric. Even more advantageously, it was possible to export paths so that they could be re-imported and copied onto the original image at a later date. This meant that in the event of a score appearing erroneous, it was possible to re-examine the original visual measurements rather than rescoring the image. Equally it was possible rapidly to evaluate large numbers of images for accuracy very quickly using the images with the paths recorded onto the original image. Due to confidentiality issues the bone scans are not displayed here, but the principle was used in the following section and an example is provided there. GIMP provided a clear advantage to both of the other methods used. 25 images were measured twice to examine reliability. The ICC (type 3) for this subsample was very high ($r = .985$). With this method it was possible to evaluate around 25 images an hour, though this was with fewer symmetry measures to be scored than in either previous sample.

2.9.2 Limitations of GIMP

It was a relatively complex process to export the data into a usable format. As the data were not stored in a format acceptable for export to a spreadsheet, a specialist spreadsheet needed to be created to import and calculate the scores appropriately. Additionally, it was necessary to standardize the order of measurements: any deviation from the standard order involved a need to start again from the beginning for that image.

2.9.3 Outcome Measure of asymmetry in the ORCADES

Initially six bones were measured. Given the high DA exhibited by two of these the final outcome measure was a mean score of all bones excluding the ulna and radius.

2.10 Improvements on previous methods of measuring asymmetry

The work described here presented significant advantages to prior methods of symmetry measurement. It allowed for measures to be taken without the measurer being aware of the scores for any of the variables with which asymmetry would be correlated. It allowed for rapid visual inspection of errors by the measurer or by another and demonstrated high levels of accuracy.

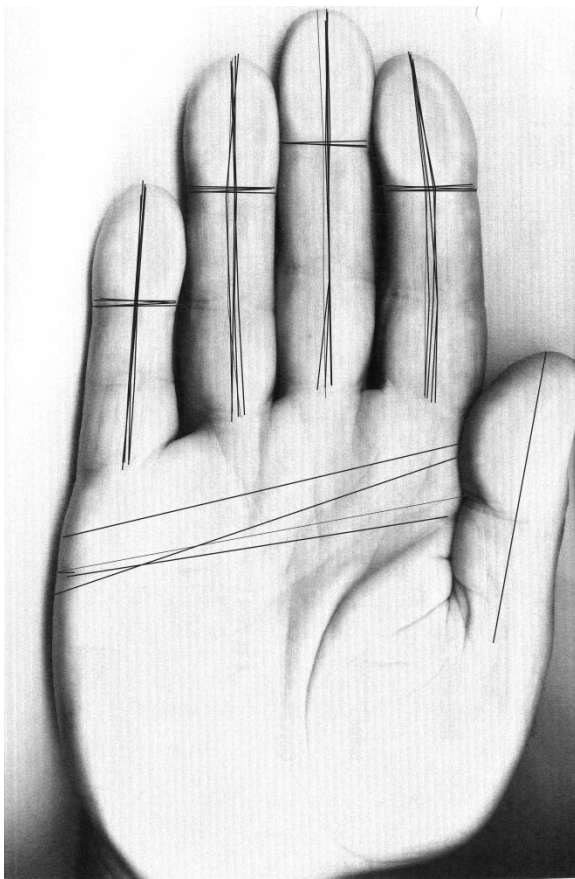
A further goal of the work was to allow for large number of participants to be scored rapidly. Digital imaging is a good tool for this given that a participant can be scored without them having to be present for measurement and it also allows for accuracy of measurement to be quickly audited. This allows part of the process to be delegated to others without any loss of accuracy, since hundreds of images can be checked for accuracy within an hour. A method to test this will be discussed presently.

2.11 Pilot Work: Remeasuring the LBC1921 handscans

As noted above, curvature of the fifth digit was problematic when attempting to measure digit symmetry via a straight line (see also fig. 2.1). Other digits were less strongly curved, but clearly not straight. This meant that curvature of all digits might be problematic with respect to accurate symmetry measures: curved digits might falsely imply high asymmetry when the total lengths of the digits are in fact very similar. A group of six undergraduate volunteers re-scored all the LBC1921 participants for symmetry of the hands. This involved two differences from the original method. Firstly, rather than measuring symmetry of only the digits, they also recorded symmetry of the breadth of the palm. Furthermore, they recorded all digits segment by segment. This was done only for the fifth digit in the original measures. This meant that all digits were measured so as to account for curvature, which was recorded separately. This measure was recorded too late to be included in analysis, but the pilot acts as a proof of concept demonstrating how measurement of asymmetry can be further improved, and was built directly upon the methods described previously in this chapter. The ICC of the six volunteers was very high when they separately rated a subsample of 20 images ($r = .910$) and they averaged around 15 participants per hour (as elsewhere type 3 ICC was used).

Excluding time for training, this means a sample size defined as good by Van Dongen and Gangestad (2011) – 350 participants – could be measured in under 4 hours by 6 volunteers. As such this presents an opportunity for future work with an experienced measurer auditing the results visually. Using GIMP it is possible to overlay the paths of multiple raters onto one image to evaluate the relative performance of each. An example of this can be found in fig. 2.6. While the measurers exhibit relatively high agreement on the lengths and widths of the digits (though there is still some disagreement in the placement at the base of the digits as opposed to the tips), there is considerable disagreement over the breadth of the palm. While normally it would be difficult to evaluate reliability (except numerically), here it can be done visually at a glance. Images such as these can be used to assist measurers in understanding their errors and how to prevent them and the level of disagreement decreased considerably over the project period.

Fig. 2.6: Six measurers score symmetry of the hand



Note: Each set of lines on a given trait indicate a different rater. There is a high level of disagreement in measuring the breadth of the palm in comparison to the digits. One measurer has – erroneously – also measured the length of the thumb.

2.12 Conclusions on Methodology

This chapter has provided essential information about each of the four samples including the sample size, background, and age. Furthermore, the existing research conducted on each sample has been briefly referenced, demonstrating the proven utility of all the samples examined in the thesis. Collectively the four samples can productively address the outstanding issues discussed in chapter 1 section 1.11.

This chapter has also demonstrated how the methods here can be used to improve upon the prior methods of asymmetry measurements outlined in chapter 1, section 1.2. The evolution of such methods over time suggests further room for improvement and that a focused body of research on asymmetry produces not just empirical findings, but methodological advances as well. As discussed in chapter 1, research on symmetry can best be characterized as broad but shallow: as shown earlier, this is often true of the methodology as well, with many different methods and few repetitions of any particular approach. The present work, with a strong focus on digital measurement, an emphasis on reliability and the capacity to measure large samples relatively quickly and efficiently, not only contributes to improvements in the practical aspects of measurement but can address theoretical problems described in chapter 1. Notably, the issue of sample size is a persistent problem because of the difficulty of measurement: the methods discussed here provide a way of overcoming this problem. The next chapter will discuss how each sample and research method address the outstanding questions set out at the end of chapter 1.

Chapter 3 – Overview of Empirical Chapters

The previous chapter demonstrated that the four samples studied in this work can be used to advance the existing literature. Combined with the methodological advances described in that same chapter, it is possible to extend our knowledge not just on empirical relationships between symmetry and other variables, but to expand the range of asymmetry measures in use. As described in chapter 1, research in the field is best characterized as broad but shallow. Consequently, the empirical work attempts to deepen our understanding of some important topics in asymmetry research, greatly improve upon past sample sizes to achieve higher power, and test areas where an association with asymmetry has been proposed but rarely empirically tested. This section briefly describes each empirical chapter.

3.1 Chapter 4 – Symmetry in Human Childhood

As discussed in chapter 1 section 1.6, symmetry across the lifecourse has rarely been explored and only once in children (Wilson & Manning, 1996). This is in spite of the fact that if symmetry is measuring fitness, changes in symmetry across the lifecourse are likely and may have a confounding effect on symmetry work that does not account for age. The outstanding research question of how symmetry varies, if at all, across human childhood, is examined in this chapter. Using a large (total $n = 887$) sample of children from the Science Festival Sample (SFS) this chapter represents the second study on a topic which has considerable implications for our understanding of the theoretical basis of links between symmetry and measures of wellbeing.

3.2 Chapter 5 – Symmetry and Intelligence

Chapter 1 section 1.7 demonstrated that research on symmetry and intelligence is one of the most heavily studied topics of symmetry. However, it is also representative of some of the larger problems in the field: a dependence on small sample sizes, effect sizes much larger in the published than the unpublished literature, and a lack of consideration for sex differences (Banks, et al., 2010). The outstanding research questions here are whether the asymmetry and intelligence association can be replicated in a large sample, whether the association can be

found endogenously as well as on the surface of the body, whether the association is influenced by important covariates such as age, and whether the magnitude of the association is similar for men and women. Despite the relatively large number of studies on symmetry and intelligence, these questions remain unanswered. They are tested here using the ORCADES dataset: with a final sample size of 491 chapter 5 tests the research questions using a sample size larger than any prior study.

3.3 Chapter 6 – Symmetry and Reaction Times

Reaction Times (RTs) have been linked to symmetry twice in studies examining adults (Penke, et al., 2009; Thoma, et al., 2006). No studies have been conducted on children. There is, therefore, a major outstanding question of whether symmetry and RTs are associated in childhood as they are (tentatively, given the very few studies on the topic) linked in adulthood. Chapter 6 is the first empirical attempt to address this issue and uses the SFS with a combined sample size of 846 children.

3.4 Chapter 7 – Minor Physical Anomalies and Cognitive Decline

As discussed in chapter 1 section 1.4, Minor Physical Anomalies (MPAs) have rarely been studied alongside symmetry despite arguments that the theoretical basis for the links between MPAs, symmetry and well being are the same. At least one prior study has shown a significant positive correlation between MPAs and asymmetry (Weinstein, et al., 1999). Given the recommendation to aggregate as many symmetry traits as possible (Knierim, et al., 2007) to improve validity, using MPAs in studies that also measure symmetry might be one way of improving the utility of the eventual measure by providing additional indicators of the same underlying variable tapped by the symmetry measures. Based on the evidence in chapter 1 and the previous two sections, the research question here is whether or not MPAs relate to cognitive ability. This chapter tests for such an association using a novel, continuous MPA. Using the LBC1921 dataset ($n = 192$) the chapter examines links between an MPA and cognitive change across more than 70 years.

3.5 Chapter 8 – Symmetry and Personality

As discussed in chapter 1 section 1.8 symmetry has been linked to personality traits, but the findings are inconsistent. The outstanding research question here is whether the previously found links between personality and symmetry are false positives or genuine. Using the LBC1921 and the Berlin Sample (the only chapter to use the latter sample) the chapter examines linear and curvilinear associations between five personality traits (Extraversion, Neuroticism, Agreeableness, Conscientiousness and Openness to Experience). This chapter is the first empirical study to test associations between personality traits and symmetry in the elderly. Across the two samples, the total sample size was 380.

3.6 Chapter 9 – Symmetry and Socioeconomic Status

Associations between symmetry and Socioeconomic Status (SES) have only rarely been tested. The only prior published study examining facial asymmetry and SES, for example, was published while the present work was being conducted (Özener & Fink, 2010) The present chapter addresses the question of whether SES is linked to symmetry and advances the prior work by assessing whether early or mid-life SES is more important and whether the findings are true for men and women. The chapter uses the LBC1921 sample, and is the first empirical study of SES and symmetry in the elderly.

3.7 Summary of Empirical Work

All of the empirical chapters contribute in some way to addressing the outstanding questions in the literature set out in chapter 1 section 1.11. In some cases they provide considerably larger sample sizes than in prior work (chapters 4 and 5), extend the work to previously understudied samples (chapters 4,6,7,8 and 9), advance existing methodology (chapters 5 and 6 especially) and often represent the first or near-first work in the area (chapters 6, 7 and 9). The empirical work begins in the next chapter with an examination of the association between symmetry and age during childhood.

Chapter 4 – Symmetry in Human Childhood

4.1 Introduction

This chapter builds on the empirical work described in chapter 1 section 1.6.1 and addresses some of the outstanding issues in symmetry research discussed in chapter 1 section 1.11. Specifically, this chapter discusses symmetry across human childhood and how better understanding of this subject can help us understand the importance of controlling for age when conducting symmetry research. It also advances the understanding of the underlying mechanisms linking symmetry and the outcome measures discussed throughout chapter 1.

To briefly reiterate, bilateral symmetry of an organism is a commonly-used measure in investigating canalization or reliability of phenotypic development despite stress (van Valen, 1962; Waddington, 1957) and the greater the asymmetry between bilateral paired structures, such as finger lengths, the lower symmetry is. Scores for a range of traits, including length of the fingers, circumference of the ankles, ear height and ear-width, can be aggregated for greater reliability. As elsewhere in the thesis although the term “Fluctuating Asymmetry” (FA) is sometimes used in the literature (van Valen, 1962) the term symmetry will be used here for convenience.

Symmetry may indicate fitness and therefore aid our understanding of other behavioural fitness indicators such as intelligence (Banks, et al., 2010; Bates, 2007; Furlow, et al., 1997), and even help understand ageing and underlying physical and cognitive decline (Penke, et al., 2009). Despite this, little is known about how symmetry alters across the lifecourse, especially its changes with development in human childhood. Only one published study examining asymmetry across this period has been identified (Wilson & Manning, 1996).

Understanding changes in symmetry across childhood is important for both practical and theoretical reasons. Symmetry is generally regarded as a measure of the lifecourse responses to stress, which should therefore accumulate over time. This implies that asymmetry should be at a minimum very early in life, with a monotonic (perhaps linear) increase over time. Data suggest that this is true in old age: higher levels of bodily (Bates et al., submitted for publication) and facial (Penke, et al., 2009) asymmetry are found in aged compared to younger samples. However, empirical data are lacking for asymmetry in early development.

If asymmetry indexes accumulated environmental impacts, it should increase across the lifecourse, perhaps increasing most rapidly very early and very late in life, paralleling the lower stress resistance (and higher mortality) in the very young and the very old (Murray & Lopez, 1997). Alternatively, if active developmental processes are present which work to increase phenotypic quality (and decrease asymmetry) during maturation (Bates, et al., submitted for publication), then asymmetry may decrease to some minimum level (perhaps early in adulthood), prior to increasing thereafter as stress is accumulated. This pattern is seen, for instance, in cognition, with fluid-type cognitive abilities increasing into early adolescence and declining later in life (Craik & Bialystok, 2006). Investigating age-associated changes in asymmetry may therefore inform theories of the evolutionary implications of asymmetry for bodily structure and function, and behaviour across the lifespan.

4.1.1 Prior Research on Symmetry in Childhood

The sole study to address changes in asymmetry during childhood to date (Wilson & Manning, 1996) investigated 680 participants between the ages of 2 to 18 years. Socioeconomic data were not specifically recorded, but the researchers believed the sample to be drawn from a variety of socioeconomic backgrounds. They identified a trend for asymmetry to reduce from age 2 until approximately age 11 followed by a short rise up until about age 15 followed by a return to decreasing asymmetry until at least age 18 (the oldest age studied). The trend was statistically significant but nonlinear. This research has significant implications in that it suggests changes in asymmetry reflect not only cumulative stress, but active processes causing asymmetry to decrease as the organism approaches important life-stages such as the end of childhood, or entering the reproductive phase. Similarly, it suggests that asymmetry may rise even early in life (i.e., ages 10–15) perhaps as a result of physical stress (including those associated with adolescence and puberty).

Gaining more certainty about the timecourse of these changes is theoretically important as it can inform researchers about the relationship of asymmetry to structural and behavioural development as well as to lifelong stress, with implications for understanding associations of evolved indicators of fitness (Thornhill & Gangestad, 2006). Methodologically complex, nonlinear changes across development suggests that controlling for higher-order components

of age (e.g. age squared and age cubed) will be an important factor as asymmetry research is expanded across the lifespan, especially beyond the common college age (i.e., about 18 to 22 years) pool that is mainly studied to date. These subjects may exhibit levels of asymmetry which are not representative of effects in much younger and much older individuals.

For these reasons, the study set out to replicate and extend research on links of asymmetry to age across an interval from age 4 to 15 years in a large ($N = 887$) and relatively socially homogenous sample of children. The study contrasted the two hypotheses which were introduced above: If asymmetry is an accumulated index of the ability to respond to stressors, asymmetry is predicted to increase monotonically with age, with the youngest children having the lowest asymmetry. By contrast, if asymmetry reflects active developmental processes generating an optimal phenotype at maturity (Bates, et al., submitted for publication) it is expected that symmetry will increase over time; i.e., a decrease in asymmetry from age 4 to 15 years.

4.2 Method

4.2.1 Participants

Participants were visitors to the 2009 and 2010 Edinburgh International Science Festivals. Full details of the sample are available in chapter 2 section 2.1.2. Since not all participants completed all measures, this sample size differs slightly from that described in chapter 7 despite the measures being taken at the same time. In 2009, 494 children aged between 4 and 15 years ($M = 9.4$, $SD = 2.3$) participated; 208 males (age $M = 9.5$, $SD = 2.4$) and 286 females (age $M = 9.3$, $SD = 2.3$). In 2010, 402 children participated (mean age = 9.4 years, $SD = 2.2$ years, range 4 to 15); 197 males (age $M = 9.4$, $SD = 2.2$) and 205 females (age $M = 9.5$, $SD = 2.1$). Informed consent for each child to participate was gained from a parent or guardian. Participation was entirely self-selecting and not all visitors participated. The 2009 study was granted ethical approval by the Faculty of Law, Business and Social Sciences faculty ethics committee of the University of Glasgow, and the 2010 study was granted ethical approval from the Psychology, Philosophy and Language Sciences ethics committee of the University of Edinburgh. Postcode information was collected for the 2009 festival, and a measure of deprivation derived from these suggested that participants were relatively socioeconomically

homogenous and of a generally more affluent background than the general population (Dykiert, et al., submitted).

4.2.2 Procedure

All data were collected by trained testers in a dedicated laboratory section of the Festival. Both hands of each participant were scanned using a digital flatbed scanner. Hands were re-scanned as necessary (typically due to motion during scanning). Motion during scanning is detectable as blur, and all blurred images were removed prior to scoring. The process for measuring symmetry is described in chapter 2 with the specific process for the science festival sample described in section 2.8 of that chapter. To briefly re-iterate, lengths and widths of the digits (excluding the thumb) were assessed using the digital-image analysis software autometric (DeBruine, 2004). For lengths, digits were measured from the lower finger crease to the tip of the finger. Width was measured by drawing a line from one side of the finger to the other across the upper finger crease. Reliability of measurement was assessed in two ways. Two separate scans of both hands were measured for three individuals who were not participants in this experiment. By calculating the intraclass correlation coefficient (ICC, type 3) between the paired images, it was possible to evaluate the reliability of the methods. Agreement for the three pairs as measured by the author were (r) .993, .989, .991, indicating high reliability. Secondly, the ICC was calculated for 25 images drawn from the sample measured twice by the author which indicated very high reliability ($r = .997$), as expected given the high resolution of the scans. While in some cases all participants are measured twice or three times and the results averaged, if high reliability is demonstrated within a subsample this is not necessary (Knierim, et al., 2007). As is typical in this area of research (Bates, 2007; Furlow, et al., 1997), asymmetry was calculated using the symmetry formula described on p21. This renders each trait difference into a percentage, standardizing scores for traits of different size. The final outcome measure was the mean of asymmetry for the eight traits (the lengths and widths of digits 2-5 of each hand). As individual bilateral traits may have unusually high or low asymmetry compared to the body's average, mean asymmetry is more representative of asymmetry across the body. Usable asymmetry data were available for 99.1% of subjects (888 subjects). One further subject had no recorded gender. All reported statistics have 887 subjects. To facilitate the evaluation of non-linear trends in the data, the predictor (age) was centred on the sample mean, reducing the

likelihood of multicollinearity in polynomial regression models (Bradley & Srivastava, 1979).

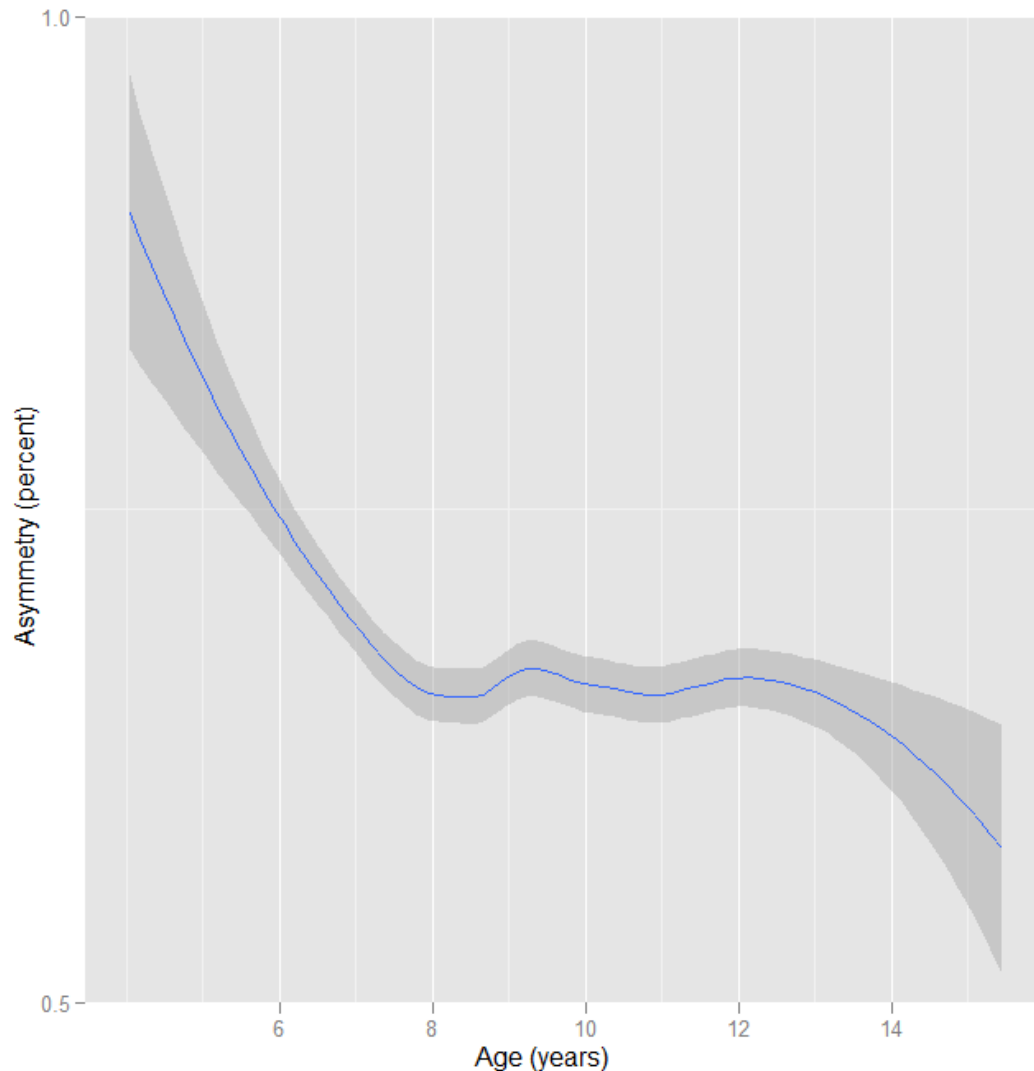
4.3 Results

Participants in the 2009 and 2010 festivals did not differ significantly in age ($t(886)$, $-.26$, $p = .79$) or level of asymmetry ($t(886)$, $-.59$, $p = .56$), and were therefore merged into one dataset. In chapter 7 different measures were used in the 2009 and 2010 festivals and so the two datasets were kept separate: by contrast, here the science festival sample can be treated as a single unit. There were no sex differences in age ($t(886)$, $.52$, $p = .60$). Mean asymmetry was .67% ($SD = .23$). Sex differences in mean asymmetry were not significant ($t(791)$, 1.73 , $p = .09$): male mean asymmetry = .69%, $SD = .25$; female mean = .66%, $SD = .22$. Sex differences in intra-individual variability in asymmetry were evaluated; that is, whether males and females exhibited differing levels of consistency in asymmetry score across the eight measures (the lengths and widths of digits 2-5). To test this, a regression model was run using the standard deviation of asymmetry as the outcome variable, and mean asymmetry and gender as predictors. Gender did not significantly predict intra-individual variability in asymmetry after controlling for mean asymmetry ($\beta = -.024$, $p = .31$).

The association between asymmetry and age is shown in fig. 4.1, which is a smoothed (loess) plot. The larger standard errors at the extremes of age in the sample reflect lower numbers of subjects in these age groups. The data showed a significant negative linear association ($r = -.10$, $df=886$, $p=.004$); older children were more symmetrical. Mean asymmetry decreased from ages 4 to 8 years, remaining approximately flat thereafter. A polynomial regression on asymmetry using powers of age (i.e., age, age², age³ and higher), as well as gender, and interactions between these terms, was tested. Gender showed no significant main or interaction effects with age or higher powers of age, and so was dropped from the model. Some higher terms were not significant, and so were dropped sequentially beginning with the highest non-significant term (in this case, age⁵), with age³ the highest remaining term in the final model. This resulted in a model where asymmetry was expressed as a cubic function of age in which age ($\beta = .019$, $p = .75$) was non-significant whereas age² and age³ were significant ($\beta = .105$, $p = .004$ and $\beta = -.162$, $p = .011$ respectively), with an adjusted R² of

.022 for the model. Overall the trend was negative, with decreasing asymmetry between ages 4 to 15 years, and most of the decline in asymmetry occurred between ages 4 to 8 years.

Fig. 4.1: Asymmetry decreases nonlinearly with age



Note: Asymmetry is measured as a percentage. Age is measured in years. Line indicates trend. Shaded region indicates ± 1 SE.

4.4 Discussion

This research identified a significant negative association between age and asymmetry; children's hands became more symmetrical with increasing age, especially from age 4 to about age 8 years. This was contrary to predictions of a linear upward trend based on error-

accumulation models of asymmetry (van Valen, 1962). That asymmetry declines, rather than increasing or remaining stable across this period of early development, is a notable finding and is one of only two studies on the topic. Both Wilson and Manning's (1996) study and the present report noted decreases in asymmetry up to age 10 years. Importantly, whereas Wilson and Manning found evidence of increasing asymmetry from ages 11 to 15 years, in this data this corresponded to a period where asymmetry remained stable. Further work is necessary to identify the cause(s) of this divergence in results.

As discussed in chapter 1, such findings mesh well with what is expected from our understanding of childhood growth. Using a common division in life history research (Geary & Bjorklund, 2000), the period from 4 to 8 years during which symmetry is enhanced is characterized as a stage in which parental care is tapered off as offspring are required to act with increasing independence as well as to interact with other children and with adults (Bogin, 1997). During this period offspring begin to eat adult-like food, with accompanying changes in dentition, though the diet remains specialized as a consequence of the smaller size of the digestive tract (Bogin, 1997). This childhood phase is also marked by rapid growth in the brain (during ages 5 to 6 years in particular), and a bodily growth spurt which, though smaller than the one experienced during puberty, is significant. Because of this patterned change in diet, growth in body and brain size, and increased social and cognitive demands, it has been suggested that this period of 4 to 8 years (over which this research has identified a peak in symmetry) corresponds to the period in which ancestral hominid offspring would have been expected to enter a post-weaning phase (Bogin, 2009). This suggests that asymmetry indexes functional enhancements underlying maturation.

This study was limited in that it only examined children up to the juvenile stage: more data on asymmetry spanning adolescence and especially the peri-pubertal period would be valuable, as this period covers the last pre-adult stage (Geary & Bjorklund, 2000).

Adolescents are preparing to enter the reproductive period and, if symmetry continues to index fitness related development (as suggested by links with IQ post-puberty: Banks, et al., 2010; Bates, 2007; Furlow, et al., 1997; Penke, et al., 2009; Prokosch, et al., 2005), an additional decrement in asymmetry might occur during this period. A replication examining participants of the same age range repeatedly over a number of years would increase confidence in these findings and provide greater validity than this cross-sectional design.

Lastly, the effect sizes exhibited here, while significant, were not large and so the importance of the findings should not be overstated.

Strengths of the present study include its sample size and the high level of socioeconomic and geographic homogeneity among the participants. The latter aspect reduces the likelihood that the result reflects confounding variables which were not controlled for in the study as the candidates were similar in many important respects. Examining age effects on asymmetry in samples where details of the socioeconomic environment are known would be valuable to assess the impact of early life factors including deprivation (Özener & Fink, 2010; Thornhill & Gangestad, 2006).

The finding that symmetry increased across early development supports the idea that asymmetry is not (only) an indicator of accumulating stress, and that active symmetry-enhancing mechanisms exist. This is compatible with data collected on asymmetry in old-age, which suggest that asymmetry is measuring developmental precision, with links of cognition to asymmetry reflecting individual differences in symmetry enhancing mechanisms active in early development (Bates, et al., submitted for publication). This matches the general trend in symmetry work described in chapter 1 section 1.3: that symmetry is indexing a measure of underlying well-being and is not simply a byproduct of an evolved preference for symmetry. A second factor highlighted by these data is the contrast between increasing symmetry observed until at least the post-weaning phase compared to subsequent increases in asymmetry, perhaps beginning as early as age 10 (although the data suggest this decline in symmetry apparent in old age may not begin until at least age 15). The sources of this contrasting pattern of developmental improvement and chronic divergence from symmetry should be studied in more detail, contrasting the role of stress and illness against active or programmed de-resourcing of developmental maintenance mechanisms in a bias towards reproductive success post-puberty. The findings confirm the need to control for age in asymmetry research, and show that symmetry does not decrease monotonically through the lifespan, but can be increased by active processes and that such processes are increasing symmetry at some, but not all, stages of childhood. This research provides support for the proposition that symmetry is an important indicator of the state of the organism. This will now be evaluated further by empirically examining links between symmetry and intelligence.

Chapter 5 - Symmetry and Intelligence

5.1 Introduction

This chapter expands upon the subject of symmetry and intelligence discussed in chapter 1 section 1.7. The key goal in this chapter is to demonstrate how symmetry and intelligence research can be expanded to novel measures of symmetry (in the present study, the bones) while addressing the outstanding issues in symmetry research examined in chapter 1 section 1.11.

Again, symmetry can be assessed by examining size differences across any bilateral paired structure: typical examples in humans are digits, ankles, and landmarks of the face (Furlow, et al., 1998; Penke, et al., 2009). This concept is often referred to as Fluctuating Asymmetry (FA), because the origins of these asymmetries are deviations (fluctuations around) average differences of zero (van Valen, 1962). However, this chapter shall simply refer to the positive manifestation of symmetry, for ease of understanding.

There is growing evidence that people with higher general intelligence (usually abbreviated as ‘*g*’; (Spearman, 1927) tend to have more symmetrical bodies (Banks, et al., 2010; Bates, 2007; Furlow, et al., 1997; Prokosch, et al., 2005). Because bodily symmetry may reflect the reliability of phenotypic development in spite of stress, higher symmetry is often interpreted as a greater capacity to follow an optimal developmental path (Waddington, 1957).

5.1.1 Prior Research on Symmetry and Intelligence

Meta-analysis of studies to date found that the association between symmetry and intelligence had an effect size (*r*) of around .16 (Banks, et al., 2010); more symmetrical individuals tend to be more intelligent. This finding has attracted interest because it suggests that some underlying characteristic of bodily processes might influence diverse cognitive and biological outcomes. Sometimes referred to as bodily system integrity (Whalley & Deary, 2001), this concept captures the idea that there might be some overall quality of functioning, or integrity, in the organism; a quality that differs between people. For system integrity to be useful in understanding individual differences—in, for example, cognition, health, and longevity—

there must be reliable and valid markers of the construct (Gale, et al., 2009). The association between symmetry and intelligence, and the association between symmetry and health (Van Dongen & Gangestad, 2011), suggest that symmetry may be such a marker. However, to date, research on the topic has been subject to a number of limitations.

The meta-analysis performed by Banks et al. (2010) identified several key issues which should be addressed before the validity of the association between intelligence and symmetry can be confirmed. Firstly, sample sizes in the published literature are too small, with an average of 134 and a maximum of 263 (Johnson, et al., 2008). As noted by van Dongen and Gangestad (2011), all studies, therefore, have been significantly underpowered to detect the likely effect sizes of approximately 0.15; 80% power for this effect size, with alpha at 0.05, requires a sample size of approximately 350.

Secondly, a variety of individual traits have been measured across studies and the equivalence of these remains unclear (Knierim, et al., 2007). Whether some traits are better at indicating underlying bodily system integrity is an important question. Where the traits that are measured vary, effect sizes may be heterogeneous, or some studies may falsely report null findings because traits used were sub-optimal. For instance, traits subject to wear and tear may begin to exhibit systematic size differences based on degree of usage (Özener, 2010). This might affect some traits (such as digits and arms due, for instance, to repetitive use in work), but perhaps not others (such as ears or facial landmarks). Understanding which traits are valid and equivalent in their quality is an important goal in the field. It would be of value, therefore, to examine symmetry and intelligence with new, arguably high-quality traits in large samples. As discussed in chapter 2, external measures of symmetry are the norm. Internal bodily symmetry of any kind has rarely been studied in humans, and examinations of bones have typically been done post-mortem (DeLeon, 2007; Gregory Livshits, et al., 1998; Van Dongen, Wijnaendts, et al., 2009) which leaves endogenous asymmetry a major untapped area for research.

Thirdly, if symmetry and intelligence are both indicators of underlying bodily system integrity, it is important to account for variables which may modify the strength of their association. For example, many existing samples draw on undergraduate college students entirely or in part, thereby examining relatively more intelligent participants (in samples with a restricted range of intelligence, which itself can lead to underestimation of the association's

effect size) with a mean age frequently in the late teens or early twenties. Because age correlates with symmetry, whereby symmetry increases as a child approaches adulthood (Manning, et al., 1997) but declines during old age (Kobyliansky & Livshits, 1989), it is important to be aware of how age and other variables influence the relationship between symmetry and intelligence. Besides age, overall status including health (Van Dongen & Gangestad, 2011) and early life circumstances (see chapter 4) associate with symmetry and may influence the relationship: of these covariates Banks et al. specifically recommend testing for age.

Fourthly, the findings suggest that sex differences in symmetry – the existence and theoretical basis of which remains a topic of active debate (Banks, et al., 2010; Penke, et al., 2009) – warrants the inclusion of both males and females in any sample, and for associations to be reported separately by sex.

The present study addresses these issues directly. The present work tests the hypothesis that higher symmetry will be associated with higher intelligence after controlling for the effects of age, birth weight (as an indicator of early status), and a history of broken bones, which can bias asymmetry scores upwards (Knierim, et al., 2007), and that the relationship will be the same for males and females. The sample size of 491 is almost twice the size of the largest single previous study (Johnson, et al., 2008). Secondly, this work measures arguably high-quality traits not previously used to assess the relationship between symmetry and intelligence. Here, the relationship between bone symmetry and intelligence is tested *in vivo*. Thirdly, the work draws on a wide age range of participants (from 18 to 86 years) to evaluate the relationship between symmetry and intelligence across most of the human lifespan, and the models also control for the hypothesised effect of bone breakages (Knierim, et al., 2007) and birth weight (Van Dongen & Gangestad, 2011) on symmetry and its measurement. Lastly, the sample size is sufficiently large to allow for sex-specific analyses.

5.2 Method

5.2.1 Participants

Participants were all drawn from the Orkney Complex Disease Study (ORCADES), a family-based, cross-sectional study in the isolated Scottish archipelago of Orkney where genetic

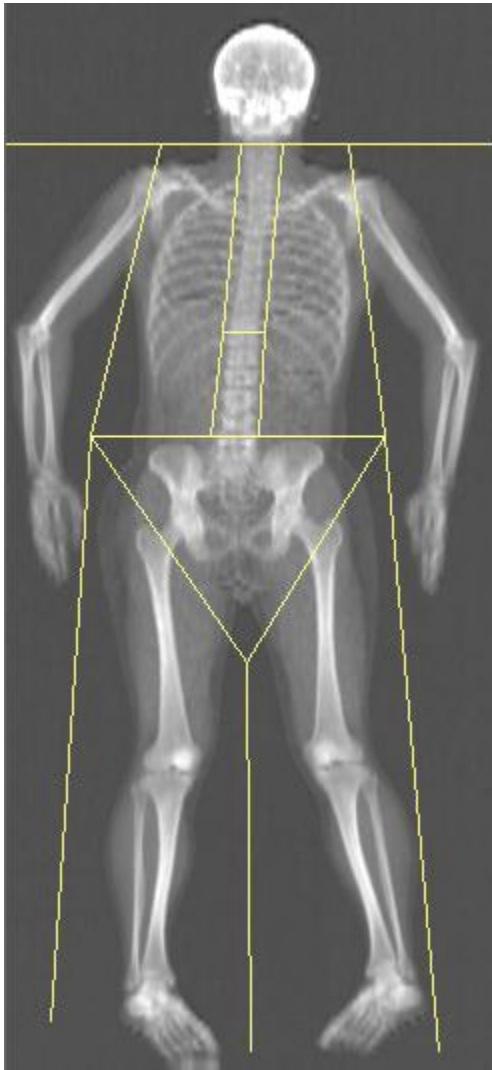
diversity in this population is lower compared to the rest of Scotland, which is consistent with high levels of endogamy historically (McQuillan, et al., 2008). Participants were drawn from a subgroup of ten islands for the study. Over 300 health-related phenotypes and environmental exposures were measured in each individual along with fasting blood samples. All participants gave informed consent and the study was approved by Research Ethics Committees on Orkney and in Aberdeen. For more details on study design, recruitment, and testing see McQuillan et al. (2008): this chapter reports here only variables relevant to the hypotheses described above. 1159 participants provided data on symmetry and intelligence. Of these, 491 provided data on all covariates described here: the loss in sample size is attributable to controlling for the additional covariates in the model (birth weight and bone breakages). These 491 participants were aged between 18 and 86 years ($M = 48.9$, $SD = 14.0$). Of these, 156 were male (age $M = 47.5$, $SD = 14.2$) and 335 were women (age $M = 49.5$, $SD = 13.8$). Symmetry, intelligence, and other measures were taken with a time gap of no greater than 18 months. Some participants were related to each other (see McQuillan et al. 2008 for more details).

5.2.2 Apparatus and Procedure

5.2.2.1 Asymmetry

Bone Mass Density (BMD) was measured at the lumbar spine, hip, and whole body using a dual energy X-ray absorptiometry (DXA) densitometer (QDR 4500, Hologic Inc., Waltham, MA). Posture was standardized for all participants. The images were of sufficiently high quality to measure the larger bones digitally (see fig. 5.1).

Fig. 5.1: Full Body Bone Scan



Note: This image is taken of a member of the original study team and is given as an example only. A version of the same image with the individual bones measured can be found in chapter 2 section 2.9.1

Six bones were measured once for each side of the body: the humerus, ulna, radius, femur, fibula and tibia. This was done using the digital imaging software GIMP (available at www.GIMP.org). Each bone length trait was measured from the uppermost to the bottommost extent of the bone. Reliability was assessed by calculating the intraclass correlation coefficient of 25 images prior to the main measurement phase (ICC type 3 = .985), which demonstrated the high reliability typical of digital measurement (Kemper & Schwerdtfeger, 2009). Whereas it is common to measure each case twice, where reliability is high only a subsample needs to be measured twice (Knierim, et al., 2007) and as such the

remainder of the sample was not re-measured. At this point, 136 images were excluded due to poor image quality. All images were measured by the thesis author who was blind to all other data from this sample prior to analysis. Asymmetry was calculated using the symmetry formula described on p21 (Bates, 2007; Furlow, et al., 1997).

Prior to analysis each bone was examined for directional asymmetry (DA). This is a potential confound which is not thought to be informative of developmental stability (van Valen, 1962). The formula described above is only informative when there is no systematic tendency for one side to be larger than the other. Where this is the case, DA is said to be present and the symmetry score is not useful for examining underlying system integrity. T-tests for DA indicated that the ulna ($t(980) = 9.42, p = .001$) and the radius ($t(980) = 4.90, p = .001$) exhibited significant directional asymmetry. In both cases the right side was larger than the left. Whereas there are multiple approaches to dealing with DA, the most straightforward option is to omit traits with DA and, where possible, utilize only traits where DA is not present (Knierim, et al., 2007). A mean asymmetry score was therefore created from the four remaining bones (humerus, femur, fibula, tibia) which exhibited no significant DA. On this asymmetry score, 0% indicates perfect symmetry, and higher numbers indicate lower symmetry and therefore a poorer outcome. Mean asymmetry was 0.52% ($SD = 0.25$). Men exhibited slightly lower asymmetry ($M = 0.49\%, SD = 0.22$) than women ($M = 0.54\%, SD = 0.26$).

5.2.2.2 Intelligence

Three cognitive ability tests were used to create a general cognitive ability factor. Firstly, in the Wechsler Digit Symbol Coding task (Wechsler, 1998a) participants had to code a series of symbols each associated with a number, with their total score indicated by the sum of correct codings in two minutes. Secondly, participants performed a Verbal Fluency test (Lezak, 1995) where they had to say as many words beginning with the letters C, F and L as possible (one minute per letter) with the three scores summed. Thirdly, they performed the Logical Memory test from the Wechsler Memory Scale: the ability to recall a paragraph immediately and after a delay (Wechsler, 1998a, 1998b): the total score was used. The Pearson correlation (r) was .43 between Digit Symbol Coding and the Verbal Fluency Total, .47 between Digit Symbol Coding and the Logical Memory Total, and .30 between the

Verbal Fluency Total and the Logical Memory Total (mean .40). A principal components analysis, when applied to these three tests, yielded a first unrotated principal component that accounted for 60.14% of the total variance. This was used as the outcome measure of fluid-type intelligence (Digit Symbol Coding loaded on to the factor at 0.83, Verbal Fluency loaded on at 0.73 and Logical Memory at 0.76).

5.2.2.3 Covariates

Besides information on age and sex, participants gave details on their background and health. Included here, because they associate with symmetry, are birth weight (Van Dongen & Gangestad, 2011) and bone breakages (Knierim, et al., 2007). Low birth weight is associated with higher asymmetry, and bone breakages can inflate asymmetry scores if not controlled for. Mean birth weight was 3.45 kg ($SD = 0.66$) with males (birth weight $M = 3.60$, $SD = 0.63$) being slightly heavier at birth than females (birth weight $M = 3.38$ kg, $SD = 0.66$). 159 participants did and 332 participants did not report experiencing any broken bones. 52 males reported a breakage (104 did not) and 107 women reported a breakage (228 did not).

5.2.3 Statistical Analyses

Regression analyses initially tested for the effects of the intelligence measure on symmetry for the combined sample, then for males, and then for females. The models were then extended to take account of the covariates of age, birth weight, bone breakage in addition to intelligence.

Historically, work in this area has tended to examine effects through regression analysis and examined sex separately without examining the differences in effect sizes between the two (see e.g. Penke et al. 2009). To ensure comparability with past research the present work follows this analytic strategy and controls for multiple comparisons with a Bonferroni correction. Alternative methods might be found outside of the field worth examining further, but they are beyond the scope of the present work.

5.3 Results

For a summary of all variables see Table 5.1. Table 5.1 includes a summary of means and SDs (or in the case of one variable, frequency) along with listwise and pairwise correlations for all variables.

Table 5.1: Descriptive statistics and Correlation Matrix of Intelligence and Symmetry Variables

	Asymmetry	Age	Birth Weight (kg)	Bone breakage	Intelligence	Mean(SD)/ Frequency with (without)	Mean(SD)/ Frequency with (without)	Mean(SD)/ Frequency with (without)
						Combined	Male only	Female only
Asymmetry	-	.178***	-.068	.069	-.111*	.52 (.25)	.49 (.22)	.54 (.26)
Age	.146 (1188) ***	-	.054	-.046	-.395***	48.89 (13.98)	47.53 (14.24)	49.52 (13.83)
Birth Weight (kg)	--.076 (491)	.057 (622)	-	-.034	-.060	3.45 (0.66)	3.60 (0.63)	3.38 (0.66)
Bone breakage	.028 (1150)	.003 (1295)	.017 (917)	-	.073	159 (332)	52 (104)	107 (228)
Intelligence	-.083 (1083)**	-.481 (1302)**	-.070 (759)	.022 (1568)	-	.24 (.92)	-.099 (.88)	.394 (.89)

*Note: * indicates $p < .05$, ** indicates $p < .01$, *** indicates $p < .001$. Correlations below the diagonal use pair-wise deletion. Correlations above use list-wise deletion. Sample size is in brackets for pair-wise deletion. For list-wise deletion, $N = 491$. For bone breakage only, value in the right most column indicates participants who have (and in brackets, who have not) had a broken bone. All other values in that column indicate means and SDs.*

Men and women did not differ significantly in age ($t(489) = -1.47, p = .14$). Women were significantly more asymmetrical than men ($t(352) = -2.18, p = .03$). Women scored significantly higher for general intelligence than men ($t(489) = -5.73, p = .001$) but exhibited a lower mean birth weight ($t(489) = 3.52, p = .001$). The more asymmetrical participants were significantly less intelligent ($r = -.11$) and significantly older ($r = .18$): see table 5.1 for full details.

5.3.1 Whole sample. Intelligence significantly predicted asymmetry ($\beta = -.11, p = .01$) when it was the only predictor. However, when expanding the model to include the covariate of age, intelligence no longer predicted asymmetry ($\beta = -.05, p = .32$), and this was also true once birth weight and bone breakage were included in the model ($\beta = -.06, p = .24$). Full details of the final models can be found in Table 5.2.

Table 5.2: Regression models predicting asymmetry

	Whole Sample	Males	Females
Age	.16 (.001)	.01 (.92)	.21 (.001)
Birth Weight	-.08 (.08)	-.12 (.15)	-.03 (.53)
Bone breakage	.08 (.08)	.15 (.05)	.06 (.25)
Intelligence	-.06 (.24)	-.24 (.01)	-.02 (.71)

Note: For model results values include standardised betas with p values in brackets. Significant values are indicated in bold. For all models asymmetry is the outcome variable.

5.3.2 Males

Intelligence significantly predicted asymmetry ($\beta = -.22, p = .006$) in the initial model.

Among men, this relationship remained significant after controlling for the other covariates ($\beta = -.24, p = .006$), none of which significantly influenced the model.

5.3.3 Females

As in the previous two models intelligence significantly predicted asymmetry ($\beta = -.11, p = .048$) when it was the sole predictor. The relationship was non-significant after controlling for the other covariates ($\beta = -.02, p = .71$), of which only age significantly influenced the model.

The effect sizes of the relationship between symmetry and intelligence (after controlling for the other covariates) were compared for males and females by converting the two partial beta coefficients into Fisher's Z scores and then testing whether the two differed significantly (McGeorge, Crawford, & Kelly, 1996). The male effect size was significantly larger than the female effect size ($p = .02$). With respect to the effect of age on symmetry the male effect size was significantly smaller than the female effect size ($p = .04$).

5.3.4 Statistical Corrections

Applying post-hoc Bonferroni corrections to the three models did not change the interpretation of the results. Among men, intelligence still significantly predicted asymmetry. While among women intelligence significantly predicted asymmetry when it was the only covariate, controlling for the other predictors rendered this non-significant.

5.4 Discussion

The present study identified an association between intelligence and bone symmetry so that those with more symmetrical bones were more intelligent. However, once additional important covariates were accounted for the picture became less clear. In the combined

sample age significantly predicted symmetry, and birth weight and bone breakages were near significant and in the predicted direction. Accounting for these variables attenuated the relationship between symmetry and intelligence in the whole sample but this is due to the differences between the sexes. For men, bone breakage was marginally non significant and the association between symmetry and intelligence was significant. For women, after controlling for the covariates, the relationship was non-significant and near to zero. Symmetry and intelligence remained significantly associated across all ages in men, but not in women.

The association between symmetry and intelligence (without covariates accounted for) is of similar effect size ($\beta = -.11$) to that observed in past research (Banks, et al., 2010). As such the traits used here are valid and equivalent to those in past research, and the findings confirm the association of symmetry and intelligence.

However, inclusion of important covariates known to associate with symmetry – especially age (Kobyliansky & Livshits, 1989; Manning, et al., 1997) – attenuated the relationship entirely in women. While some have argued that the sex difference is derived from the greater need of males to exhibit quality and so obtain reproductive success (Prokosch, et al., 2005), intelligence predicts symmetry in women when no other variables are accounted for. As such, it may be that something more complex is occurring whereby different covariates (such as age, which had a significant influence on the model among women but not men) influence symmetry differently for each sex. If men need to signal the relationship between symmetry and intelligence more clearly (so as to advertise their quality as a reproductive partner), this would also be expected to be true for other important variables (such as age), but women exhibit a significantly stronger relationship between age and symmetry.

There is a notable tendency for high intelligence to associate with a diverse range of positive outcomes (Deary, 2008), which suggests that the association between symmetry and intelligence may exist because symmetry is measuring overall welfare, which is in turn partially linked to intelligence. As such symmetry may be weakly tied to intelligence specifically. Symmetry associates with multiple measures of overall well being including health, birth weight (Van Dongen & Gangestad, 2011) and socioeconomic status (Hope et al., in press; Özener & Fink, 2010) among others, supporting this possibility.

The present study has several advantages. The large sample size means the null result among women is unlikely to be due to low power. The wide age range is an important advantage and demonstrates the need for representative samples: the fact that controlling for age attenuates the relationship in women is an important aspect of the findings and could not be achieved in a narrow age study. The study has uniquely advanced study of the association between symmetry and intelligence to include endogenous measures of symmetry, showing the association persists even in important structures such as the bones. As discussed in detail in chapter 1, while there are important theoretical and practical considerations with regards to choice of symmetry measures, there is little agreement on the degree to which different traits should yield different levels of asymmetry. The use of endogenous symmetry is a significant advancement over past work because it accesses important internal structures (in this case, the bones) rather than superficial characteristics (such as the distance between the edges of the lips). The fact that internal and external measures of asymmetry both predict intelligence would tend to argue that with regards to symmetry, any trait is acceptable. However, two of the six bone traits exhibited directional asymmetry: identifying a list of traits that typically exhibit directional asymmetry would allow for researchers to avoid unsuitable traits and thereby ensure the number of items remains as high as possible.

Future work should test the association of intelligence and symmetry in the context of other important covariates (education, health, and background status may be relevant) to assess whether the relationship is genuine or simply identifying the link between symmetry and the variety of positive outcomes associated with higher intelligence. Assessing the cause of the sex difference in the relationship is especially important as it may have theoretical implications for our understanding of system integrity. This study demonstrates that there is a link between endogenous symmetry as measured in the bones and intelligence, but also suggests that this relationship may be at least partly explained by an association between symmetry and overall wellbeing, rather than intelligence specifically. This possibility can be partially tested by examining attributes associated with intelligence. Chapter 6 will advance the present study by examining links between symmetry and Reaction Times (RTs).

Chapter 6 – Symmetry and Reaction Time

6.1 Introduction

The previous chapter reviewed support for links between symmetry and intelligence. However, as discussed in chapter 1 sections 1.3 and 1.7, the most commonly proposed theoretical argument for such links suggests symmetry should be associated with a range of important cognitive and physical attributes, not just intelligence. This chapter extends the work introduced in chapter 1 section 1.7 on Reaction Time to a new age group.

Meta-analysis suggests that the association between symmetry and intelligence has an effect size (r) of around .16 (Banks, et al., 2010; Bates, 2007; Prokosch, et al., 2005) with more symmetrical individuals tending to have higher intelligence. Combined with evidence that symmetry increases as children approach adulthood (see Wilson & Manning, 1996, and chapter 4) but subsequently declines in old age (Kobyliansky & Livshits, 1989; Penke, et al., 2009), this suggests some insight into the causes of individual differences in physical and cognitive ability and their development may be gained by exploring the association of symmetry with other intelligence-related variables early in life; this chapter examines the association between symmetry and Reaction Time (RT) in childhood.

6.1.1 Reaction Times and System Integrity

Both simple (SRT) and choice reaction times (CRT) are associated with intelligence (Bates & Stough, 1998; Deary, Der, & Ford, 2001; Jensen & Munro, 1979) with effect sizes (r) around twice the magnitude of those found for symmetry and IQ (i.e., around -.4). Shorter RTs are associated with higher intelligence. In addition to mean RT, lower variability of RT across trials is also associated with higher intelligence (Deary, et al., 2001; Jensen, 1992).

Importantly, both intelligence (Deary, 2008) and RT (Deary & Der, 2005a) are associated with longevity, with RT accounting for most of the association of intelligence with longevity (Deary & Der, 2005a). One explanation of the association of intelligence with mortality has implicated health-oriented behaviours chosen by more intelligent people throughout life as accounting for better health outcomes in brighter people (Lynch, Kaplan, & Salonen, 1997). The finding that RT is at least as strong a predictor of mortality as tests of reasoning supports

an alternative (though not exclusive) suggestion, namely that intelligence and mortality are related not only via health choices, but also via their both being indicators of an underlying property that has been referred to as bodily 'system integrity' (Whalley & Deary, 2001). RT would then be viewed as a proxy for system integrity. Consistent with this view, and similarly to mortality risk itself, RT follows a U-shaped curve across the lifespan: it is slower in childhood and old age, and optimal during adulthood (Koga & Morant, 1923; Wilkinson & Allison, 1989).

If such a latent trait of system integrity exists, then markers of system integrity should associate with health, with cognitive ability, and with each other (Gale, et al., 2009). Therefore, because both RT and symmetry (Benderlioglu & Nelson, 2004; Knierim, et al., 2007; Manning, et al., 1997; Waynforth, 1998) are markers of system integrity, RT should in turn be linked to symmetry. An association of symmetry with faster and less variable RT in childhood, then, would further support the idea that symmetry and RT are markers of system integrity. It would also buttress the idea that some causes of lifespan system integrity and longevity are present early in development, prior to both adult lifestyle choices and the onset of the chronic diseases that are responsible for most adult mortality. Finally, as Gale et al. (2009) argued, the utility of system integrity in scientific understanding of life-course development depends on the availability of robust markers of this construct. As both symmetry and RT are easy to measure, an association between the two in childhood would support their utility as early developmental markers in life-course research.

6.1.2 Empirical Research Linking Symmetry and Reaction Times

Only two studies have tested the links of symmetry with RT. Thoma et al. (2006) showed that higher symmetry was associated with faster simple and choice reaction times in a very small sample of 21 right handed male adult subjects. The other study examined facial symmetry and RT in 216 eighty three-year old subjects (Penke, et al., 2009). Higher facial symmetry was significantly associated with faster and less variable CRT in men, but not in women, and did not correlate with SRT or SRT variability. These two studies tentatively suggest that higher symmetry may be associated with faster CRT. Sample sizes have been too small to allow strong conclusions about what are predicted to be modest effects (Banks, et al., 2010).

It remains unclear whether effects are restricted to CRT, or if they are simply larger in CRT than SRT or variance measures, and present at all, whether the effects are found in females.

This chapter examines a large (total $n = 856$) sample of children across two studies, with roughly equal numbers of males and females. Examining children in this context is especially important, as RT improves (response times become lower) during childhood alongside the overall maturation of the organism, and symmetry increases during the same period (see chapter 4). Because symmetry and RT are both suggested as indicators of system integrity, it is hypothesised that more symmetrical children will exhibit faster, less variable CRTs.

6.2 Study 1: Science Festival Sample from 2009

Full details of samples 1 and 2 can be found in chapter 2 section 1.3, and details of the method can be found in chapter 2 section 1.8. As stated in chapter 2 not all participants completed all measures. As such the sample size here differs slightly from that described in chapter 4 despite them being drawn from the same overall sample.

6.2.1 Participants

Participants were visitors to the 2009 Edinburgh International Science Festival. Here, only data for participants who completed measures of symmetry and RT are described. 497 children participated and supplied usable data for symmetry and RT assessments. They were aged between 4 and 15 years ($M = 9.41$, $SD = 2.30$); 210 were males (age $M = 9.49$, $SD = 2.34$), and 287 were female (age $M = 9.36$, $SD = 2.27$). Informed consent for each child's participation was obtained from a parent or guardian. Postcode information obtained for this sample was used to examine deprivation, and the results suggested that participants were relatively socioeconomically homogeneous and on average more affluent than the general population (Dykiert, et al., submitted).

6.2.2 Apparatus and procedure

6.2.2.1 Asymmetry

Both hands of each participant were scanned using a digital flatbed scanner, and were re-scanned where poor images occurred (typically due to motion while scanning). Lengths and widths of the digits (except the thumb) were assessed with digital-image analysis software. Reliability was assessed jointly for studies 1 and 2 and found to be high. The intraclass correlation coefficient was .993, .989, .991 for three paired images, and .997 for a 25-image subsample measured twice by the author. As in most other studies in this area (Bates, 2007; Furlow, et al., 1997), symmetry was calculated using via the symmetry formula described on p21 which, when multiplied by 100, gives a percentage of symmetry with higher numbers indicating greater asymmetry. It also standardizes scores for traits of different sizes. The final outcome measure, the mean symmetry score, is an average of the symmetry scores for the eight traits.

6.2.2.2 Reaction times

In Study 1, simple and 4-choice reaction time were measured using upgraded versions of the testing devices used for the UK Health and Lifestyle Survey (HALS); see Cox, Huppert and Whichelow (1993) for information on the study and Deary, et al. (2001) for more information on the device. The device had a screen to present stimuli, and five response buttons labelled 0 to 4. During SRT trials, the central button (0) was operated by a finger on the preferred hand. For SRT trials, a “0” (zero) appeared in the small liquid crystal (LCD) display and participants were instructed to press the 0 button as soon as the stimulus appeared. All participants completed eight practice trials followed by 20 experimental trials. In the 4-choice CRT task, a number between 1 and 4 would appear in the LCD and the participant was instructed to press the appropriate response button. Buttons 1 and 2 were operated with the middle and index finger of the left hand, and buttons 3 and 4 with the same fingers of the right hand. Eight practice trials were given, followed by 40 test trials. All subjects received the same sequence of CRT stimuli. On both tasks, the inter-trial interval varied from 1–3 seconds. The tasks were presented in a fixed order: SRT preceded CRT, and response latency was recorded automatically for each trial. All data were collected by trained testers in a laboratory section of the festival.

RT data were processed as follows. Incorrect scores were excluded, along with pre-presses (RT scores of zero), and responses of < 100 ms and 150 ms for SRT and CRT, respectively.

Very slow responses were also excluded (for SRT > 3000ms, CRT > 5000ms). Subjects with > 25% missing trials were removed. Each year of age (between 4 and 15) constituted its own age band for further, age-specific exclusion criteria. Trials with RTs greater than 5 SD above the mean for that age group were removed, as were participants with mean scores more than 3 interquartile ranges above the age-specific third quartile. As a result of these screening processes 80 participants were removed and the 497 participants described above remained. Four RT outcome measures were calculated: mean SRT and 4-Choice CRT, and the standard deviation for each participant's scores across all valid trials for CRT (CRT-SD) and SRT (SRT-SD). RT scores for the four measured variables can be found in table 6.1.

6.2.3 Statistical Analyses

Regression analyses initially tested for the effect of the RT variables on symmetry in four separate models (one for each RT variable). Then the effect of RT on symmetry was retested while controlling for the effects of sex and age, as well as the 2nd and 3rd order powers of age.

6.3 Results

There were no sex differences in age ($t(442)$, $p = .54$). Mean asymmetry across the whole sample was 0.70% ($SD = 0.43$). There were no sex differences in asymmetry ($t(442)$, $p = .69$: male mean asymmetry = 0.71% ($SD = .44$), female mean asymmetry = 0.69% ($SD = 0.42$), nor in RT, either for simple or choice RT ($t(441)$, $p = .49$ and $t(456)$, $p = .26$ respectively). Sex differences in intra-individual variability in RT scores were tested by running regression models using the standard deviation for each RT variable as the outcome while controlling for the mean RT score of that same RT variable and gender. There were no significant sex differences ($\beta = 0.06$, $p = .06$ and $\beta = 0.03$, $p = .16$ for SRT-SD and CRT-SD respectively).

The core hypothesis was then tested: that symmetry would be associated with faster RTs. Initially only the four RT variables were used as predictors, with one RT variable per model. Mean CRT was significantly associated with asymmetry ($\beta = 0.09$, $p = .04$). Participants with more symmetrical hands tended to have faster mean CRT. However, this was not true for mean SRT, SRT-SD or CRT-SD ($\beta = 0.06$, $p = .15$, $\beta = 0.09$, $p = .051$ and $\beta = 0.05$, $p = .23$ respectively), though for all four variables the direction of the relationship was the same. The

analysis was extended to include the effects of age, age², age³ and gender. This did not influence the significance or direction of the effect of CRT, SRT, SRT-SD or CRT-SD ($\beta = 0.17$, $p = .03$, $\beta = 0.06$, $p = .27$, $\beta = 0.08$, $p = .12$ and $\beta = 0.03$, $p = .63$ respectively. The results of the models controlling for the covariates of age², age³ and gender are summarized in table 6.1.

A follow up study using similar methods, and drawing on children with the same demographic characteristics, was conducted the following year and is described now as Study 2.

Table 6.1: Means and SDs for Reaction Time scores and models predicting asymmetry for Study 1 and Study 2

	SRT	SRT-SD	CRT	CRT-SD	CRT controlling for CRT-SD	CRT-SD controlling for CRT
Study 1 ($n = 497$)	366 (82)	102 (58)	776 (223)	184 (99)		
Study 1 Model results	0.06 (.27)	0.08 (.12)	0.17 (.03)	0.03 (.49)		
Study 2 ($n = 359$)			673 (179)	159 (56)		
Study 2 Model results			0.16 (.045)	0.22 (.001)	0.002 (.985)	0.22 (.006)

Note: SRT = Simple Reaction Time. SRT-SD = Simple Reaction Time, Standard Deviation. CRT = Four Choice Reaction Time. CRT-SD = Four Choice Reaction Time Standard Deviation. All scores are in milliseconds. For the Study 1 and Study 2 rows, the four RT variable values represent the mean, with SD in brackets. For each study n indicates the sample size. For model results values include standardised betas with p values in brackets. For all models age, age², age³ and gender were covariates, and asymmetry was the outcome measure. Significant values are indicated in bold.

6.4 Study 2: Science Festival Sample from 2010

6.4.1 Participants

Study 2 was conducted to attempt to replicate the findings of Study 1. It was conducted at the same location (the Edinburgh Science Festival) one year later, in 2010. Participants were all children visiting the festival. A total of 359 children completed the symmetry and RT tasks. Participants were aged between 4 and 15 years ($M = 9.45$, $SD = 2.13$); 174 were male (age $M = 9.36$, $SD = 2.15$), and 185 were female (age $M = 9.53$, $SD = 2.11$).

6.4.2 Apparatus and procedure

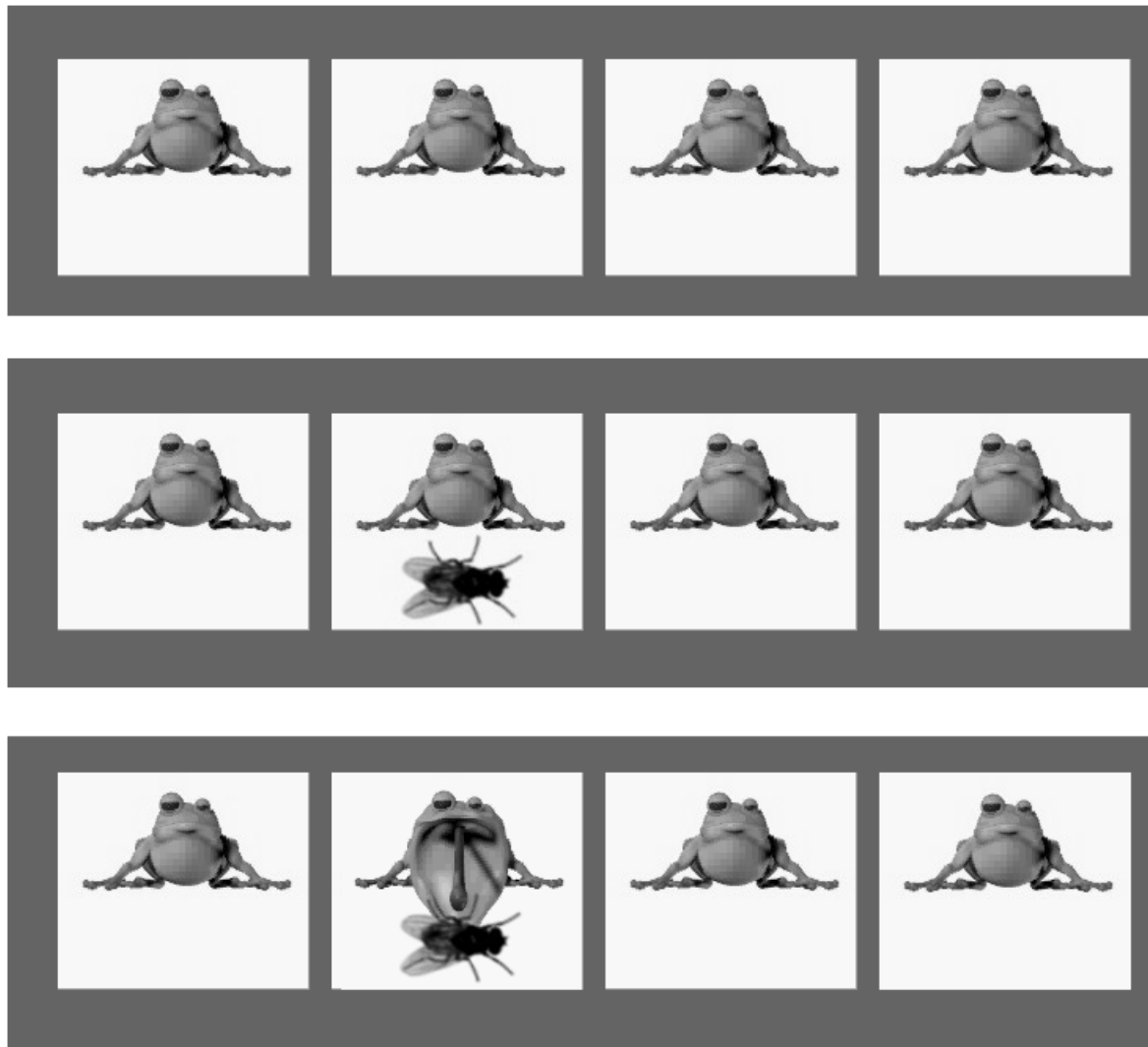
Study 2 utilized an identical procedure for the collection of asymmetry data. The RT data were collected using a new computerized RT task (a children's version of the Deary-Liewald reaction time task) which had been validated against the RT box measure used in study 1. Further details of this new task can be found in Deary, Liewald and Nissan (2011). The particular version used here used more child-oriented stimuli, with all other aspects of the task being the same as that described in Deary et al. (2011).

The Deary-Liewald reaction time task was run on a computer monitor with a 60 Hz refresh rate. Only CRT and CRT-SD were recorded; SRT was not tested. Eight practice trials were given, followed by 40 experimental trials. On each trial four white boxes were displayed horizontally across the middle of the screen against a dark blue background. In each box there was a frog (see fig. 6.1). After an interval of 1-3 seconds (selected randomly from this range) a fly would appear randomly in one of the four squares. This was the stimulus: the participant had to press the corresponding response key to complete the trial correctly. If the participant entered the correct response, the frog would appear to swallow the fly (see fig. 6.1, final panel). If the response was incorrect the fly would disappear. This visual presentation was designed to make the task more engaging for children. The software logging recorded the RT and whether the correct key was pressed for each trial.

The keys used were 'z' (to select the far left square), 'x' (second from left), the 'comma' key (second from right) and the 'full stop' key (far right). In all cases, participants rested the

index and middle fingers of the left hand on the 'z' and 'x' keys, and the index and middle fingers of the right hand on the 'comma' and 'full stop' keys.

Fig. 6.1: Deary-Liewald Reaction Time Task for Study 2.



Note: top-most image represents pre-stimulus phase. No response is required. Middle image describes the stimulus phase. Here, participants would need to select the 'x' key to indicate a correct response. Any other presses would be recorded as incorrect. In the bottom image, the program indicates a correct response: the frog eats the fly. This version of the Deary-Liewald task (Deary, et al., 2011) is designed for children and presents different images from those of the adult version.

Means and SDs for each participant were automatically computed, with only valid trials included in the results. Pre-presses (RT scores <0ms) were discarded, as were extremely fast (<150ms) and slow responses (>5000 ms). Participants with >25% missing trials were removed. Trials with RTs higher than 5 SD above the mean for their age in years were removed, along with participants with mean scores more than 3 interquartile ranges above the age-specific third quartile. After these screening processes 84 participants were removed, leaving 359 participants. Means and SDs can be found in table 6.1. The relatively faster, and somewhat more homogeneous reaction times exhibited here in comparison to Study 1 also reflect the findings of Deary et al. (2011) from adults, in which they compared the computerised task and the response box used in Study 1.

6.4.3 Statistical Analyses

As in Study 1, the models examined whether higher asymmetry scores were associated with faster and less variable RT scores. Regression analyses initially tested only for the effect of the RT variables on asymmetry (CRT and CRT-SD in two separate models). Following this the data was re-analysed and the effect of age, age², age³ and gender on asymmetry was controlled for. Lastly, as the two RT variables were both significantly associated with symmetry and were highly correlated ($r = .75$), two additional regression models were run where each RT variable controlled for the effect of the other to examine whether mean CRT and CRT-SD were separate sources of prediction or not. These final models used asymmetry as the outcome variable and controlled for the covariates described above. Full details of the models including the covariates can be found in table 6.1.

6.5 Results

The two genders did not differ in age ($t(355)$, $p = .46$). Mean asymmetry was 0.68% ($SD = 0.23$), and males and females did not differ in mean asymmetry ($t(334)$, $p = .11$); males = 0.70% ($SD = 0.25$), females = 0.66 ($SD = 0.21$). There were no sex differences in CRT (correct) scores ($t(356)$, $p = .44$). To test for sex differences in intra-individual variability in CRT scores a regression model was run using the standard deviation of CRT across all valid trials as the outcome variable, with mean CRT and gender as predictors. Gender did not significantly predict intra-individual variability in CRT ($\beta = 0.007$, $p = .19$).

Next, the hypothesis that symmetry would be associated with faster, less variable RT was tested. The initial models included only the RT variables as predictors (mean CRT and CRT-SD in two separate models). As predicted, mean CRT was again associated significantly with symmetry ($\beta = 0.16$, $p = .002$) with more symmetrical children exhibiting faster RT.

Furthermore, CRT-SD was significantly associated with symmetry ($\beta = 0.22$, $p = .001$): more symmetrical children had less variable RT. Re-running the analyses while including the covariates described above did not change the significance or direction of the effect for mean CRT ($\beta = 0.16$, $p = .045$) or CRT-SD ($\beta = 0.22$, $p = .001$). After controlling for the effects of these covariates and the effect of CRT-SD, mean CRT did not significantly predict symmetry ($\beta = 0.002$, $p = .99$). After running a model with the same covariates but this time controlling for the effect of mean CRT, CRT-SD remained a significant predictor of symmetry ($\beta = 0.22$, $p = .006$).

6.5.1 Statistical Corrections

In previous research Bonferroni corrections have not been applied when modelling links between RT variables and asymmetry (see e.g. Penke et al. 2009). Applying such corrections here meant only CRT-SD was significantly associated with asymmetry, though CRT was only marginally non-significant. As such a more conservative analytical approach might suggest variability, not mean differences, is the important RT variable associated with asymmetry.

6.6 Joint Discussion of Studies 1 and 2

In both study 1 and study 2, a significant association between symmetry and RT was identified such that more symmetrical children tended to have faster CRTs. In study 2, but not study 1, more symmetrical children also showed significantly less variance in CRT. In study 2, when controlling for the effect of mean CRT, CRT-SD continued to predict symmetry significantly, but when controlling for the effect of CRT-SD, mean CRT no longer predicted symmetry. This may mean that particular attention should be given the variability and not just mean RT scores. These findings lend support to the suggestion that symmetry and RT are both markers of system integrity, and therefore the findings here are important in

advancing the utility of system integrity in understanding life-course physical and cognitive change (Gale, et al., 2009).

The findings are compatible with those of Penke et al. (2009), who found higher facial symmetry was associated with faster and less variable CRT, but not SRT in an aged sample. This suggests that at least some measures of RT associate significantly with symmetry across most of the human lifespan, from at least age 4 to age 83.

6.6.1 Links to Past Research

Of three studies now available (Study 1, Penke et al, 2009 and Thoma et al.2006) only one has reported a significant association between symmetry and SRT. The two null effects (Study 1, Penke et al.2009) both used a dedicated simple RT device as described in Study 1. By contrast, the SRT procedure used by Thoma et al. (2006) involved choosing which hand to respond with, rather than which button to select. As such it is possible a difference in methods may explain the difference in findings, with the Thoma et al. (2006) procedure involving an element of complexity and choice not present in the box-based, more conventional SRT procedure used in Study 1. Alternatively, the relationship between SRT and symmetry may be restricted to adolescence and early adulthood (i.e. the period of lifetime optima for both measures). Power issues may also be relevant: correlations of CRT with IQ tend to be larger than those for SRT, reflecting the increased complexity of information processing involved in each response (Jensen, 1998). It is also important to note that the direction of the effect was the same for SRT, SRT-SD, CRT and CRT-SD, and effect sizes were broadly similar (see table 6.1): replication with larger sample sizes will clarify whether the association between SRT and symmetry is weaker or genuinely not present. Given that only three studies are described here, each with a very different sample mean age, and somewhat different methods, the causes of these differences cannot be identified with certainty.

Penke et al. (2009) found no significant association between RTs and asymmetry in a combined sample: only when analysing each sex separately was an association found (in men only). Thoma et al. (2006) did not examine females. In the study by Penke et al. (2009), the sample subjects' mean age was 83 years and significant sex-linked attrition effects occur due to sexual dimorphism in mortality. As this sample is larger and unselected, it seems plausible

that the symmetry-CRT link is present in both genders. The present two studies, then, confirm that greater symmetry is associated with faster (and possibly less variable) CRT times, and extend the finding into childhood, a subject group not previously studied. More broadly they confirm the association between symmetry and cognition described in chapter 1 section 1.7.

6.2 Strengths and Limitations of the Studies

A strength of the present studies was their relatively large sample sizes. In addition, homogeneity of socioeconomic status (SES) reduced the likelihood that the results reflect an unmeasured confounding variable altering both symmetry and RT. The range restriction consequent on this limited SES range may also lead to the effect sizes found in the present studies being under-estimates of the population effect sizes. As few children were included in the ages entering adolescence and the reproductive period it would be of value to extend data collection into this range, especially given evidence that both symmetry and RT reach an apogee at this time (Koga & Morant, 1923; Wilkinson & Allison, 1989; Wilson & Manning, 1996) which is supported by the evidence in chapter 4. Equally, it would be useful to explore further the symmetry and RT associations in the elderly. If symmetry and RT associate equally strongly across the life-course this would further support the proposal that they are indicating a stable life-course trait of system integrity. If, however, the magnitude of the relationship varies over the life-course, this would suggest that symmetry and RT are associated with different underlying traits.

However, there were limitations in the present work. This study examined children of different ages rather than following the same children over time. A design that retested the same children over intervals of one year or more would increase confidence in the findings. Secondly, the effect sizes observed here were modest. While consistent with findings elsewhere in the thesis and in large-scale meta-analyses of associations with symmetry and other variables (Banks, et al., 2010; Van Dongen & Gangestad, 2011) this suggests either that whatever mechanisms underlies the association explains relatively little of their shared association or that current methods of assessing symmetry are limited. Either way, it is a contrast to earlier accounts of symmetry research with reported effect sizes (in this case for intelligence and asymmetry) of up to $(r) = -.49$ (Thoma, et al., 2006).

These findings provide empirical support for the hypothesis that RT tasks and symmetry both indicate underlying bodily system integrity. Symmetry may indicate system integrity by reflecting the total stress received by the organism, or the organism's capacity to follow their original genetic 'blueprint' in a precise way. Importantly, the fact that symmetry and RT are associated in childhood indicates that the relationship is not due entirely to illness or injury in adulthood, or by differences in lifestyle or access to health and educational facilities during late childhood or adulthood. The correlation of two markers associated with system integrity during childhood suggests that cognitive and physical abilities across the lifecourse are, at least in part, influenced by processes in early development. Understanding early development, then, is important for understanding the trajectory of physical and cognitive development across the life-course.

As discussed in chapter 2 generating large numbers of symmetry measurements per participant can be difficult. However, some tools used to measure symmetry – such as digital photographs – may also be used to score participants for Minor Physical Anomalies (MPAs). Obtaining more measures of the proposed underlying construct of wellbeing improves reliability. Having demonstrated links between symmetry and cognition in chapters 5 and 6, the next chapter will explore the utility of measuring MPAs alongside symmetry by investigating links between cognition and MPAs. If MPAs relate to cognition as symmetry has been shown to in this and the preceding chapter, MPAs may be worth incorporating into studies like the one in the present chapter.

Chapter 7 – Minor Physical Anomalies and Cognitive Ability

7.1 Introduction

The previous two chapters have demonstrated links between cognitive ability and symmetry. The present chapter evaluates how symmetry research can be improved by expansion to include related concepts such as Minor Physical Anomalies (MPAs). The present chapter tests links between MPAs, intelligence, and cognitive decline.

MPAs are small, distinctive bodily features that do not impair everyday functioning, but that may be indicative of congenital disorder (Compton & Walker, 2009) or of stress and inflammation accumulated over the lifespan (Flatt, 2005). Here the association of a well-established MPA with cognitive ability and cognitive decline is tested.

Such anomalies are diverse in nature and can occur anywhere on the body. For example, humans typically exhibit only a single hair whorl (sometimes referred to as a crown), and the presence of two (or more) hair whorls is considered anomalous. Similarly, a flat and narrow roof of the mouth is unusual, as are malformed ears or large gaps between digits (Waldrop, et al., 1968). Such traits are usually categorized as anomalous only where they are distinctively different from what would be found in the general population (Waldrop, et al., 1968).

7.1.1 Minor Physical Anomalies, Behaviour, and Mental Health

MPAs are positively correlated with a number of behavioural patterns or disorders including Down's syndrome (Waldrop, et al., 1968), greater emotionality and in some but not all cases extraversion (Paulhus & Martin, 1986), and schizophrenia (Compton & Walker, 2009). Meta-analyses of the link to schizophrenia (Weinberg, et al., 2007) and autism (Ozgen, et al., 2010) suggest large effect sizes (Cohen's $d = 1.13$ and 0.84 respectively) irrespective of the site of the MPA. The fact that MPAs linked to cognitive impairment are not restricted to particular body regions suggests that MPAs may reflect problems affecting the entire system. Notably, the fact that MPAs are found to be higher among children with serious disorders such as Down's syndrome or autism (Ozgen, et al., 2010; Waldrop, et al., 1968) suggests that MPAs may be indicating shared underlying physical and cognitive problems. At least one study has shown that the severity of MPAs can increase with age (Lloyd, et al., 2003), indicating MPAs

are not restricted to indicating problems in early life and can change in magnitude over time. Combined with evidence that more frequent MPAs are associated with lower intelligence (see e.g. Rosenberg & Weller, 1973) and that intelligence declines with ageing (Deary & Der, 2005b) it is plausible that the increased level of MPAs in the elderly is indicating increased cognitive as well as physical problems during the ageing process. Such a relationship is predicted from the “common cause hypothesis” of aging, suggesting that cognitive and non-cognitive declines in old age share one or a small number of “common” causes (Christensen, Mackinnon, Korten, & Jorm, 2001). This shared factor has been conceptualised as system integrity or general fitness (Deary, 2008; Prokosch, et al., 2005). Common cause models share features with the concept of developmental stability described by Waddington (1957) as such an organism’s ability to develop normally despite the presence of perturbations. These perturbations include malnutrition, pathogens, environmental toxins and illness, among others. Greater developmental instability (DI) would be expected to lead to more severe MPAs.

While DI is usually considered in terms of early development—indicating a system which was initially poorly put together—DI may also emerge over the lifespan as a consequence of poor buffering against environmental perturbations such as high allostatic load (McEwen & Stellar, 1993). Because both early (Barker, 1995, 2007; Marmot, 2010) and accumulated (Seeman, Epel, Gruenewald, Karlamangla, & McEwen, 2010) stress have been proposed as causes of physical, sensory and cognitive decline (Christensen, et al., 2001), MPAs may form a valuable marker of health and decline among older people. Here the association of a well-established MPA – finger curvature – with cognitive ability and cognitive decline is tested. Of course MPAs would not be expected to cause age-related decline, but rather to function as a readily-measured indicator of the causes of cognitive decline.

7.1.2 Minor Physical Anomalies and Intelligence

Previous research relating MPAs to cognition has been restricted to younger samples, and sample sizes involved are typically small or recruited on the basis of conditions such as schizophrenia which might independently influence scores. Rosenberg and Weller (1973) reported a negative association of MPAs with verbal (but not spatial) intelligence, a finding replicated by Pine, Shaffer, Schonfeld, and Davies (1997) in 118 male adolescents who had

previously been evaluated at age 7 and had not, at the time of the study, been referred for psychiatric treatment. Gally, Kantola-Sorsa, and Granström (1988) found higher numbers of MPAs were associated with lower Wechsler Preschool and Primary Scale of Intelligence scores in 108 children of epileptic mothers and 100 control children (a non-verbal intelligence measure, the Leiter International Performance Scale, did not associate significantly with MPAs) in either group. Dimambro et al. (2008) found that in a sample of people with schizophrenia, MPA count was associated with lower intelligence. Importantly, MPAs were also associated with a greater decrease in intelligence over time in this sample. One study (Marcus, et al., 1985) identified no association between intelligence and MPAs, though they suggested low sample size might have been a factor (the total sample size was 100, of which 27 exhibited no anomalies and only seven exhibited three anomalies). In summary, most studies, but not all (c.f. Marcus, et al., 1985), have reported significant negative associations between MPA count and intelligence, particularly verbal intelligence.

Whereas many MPAs appear early in development and are stable across time (e.g., syndactyly, where digits are at least partially fused together), biological variation believed to underpin other MPAs accumulates during aging (Lloyd, et al., 2003). Hence, the frequency and severity of some MPAs increases with age. As with cognitive aging itself, the causes of MPAs accumulated during adult life (rather than early in development) are not well understood. It is possible that an inability to maintain basic bodily processes might lead to a failure to maintain outward systems so that age-related MPAs exhibit more clearly initial underlying stress. MPAs which accumulate or even appear *de novo* in old age may be consequences of factors occurring early in development. If this is the case, MPAs in old age should predict early cognition, as well as lifespan cognitive decline. Alternatively novel or increasing anomalies such as curvature may reflect accumulating new stresses such as damage and inflammation which accumulate independently of initial developmental state. In this case, MPAs are expected to relate to differences in rates of cognitive decline, and that this would not be accounted for by initial cognitive status.

MPAs, then, are promising aging biomarkers which are readily recorded, and have potentially tractable biological pathways. However, MPAs have typically been scored categorically – for example, large gaps between digits might be categorized as abnormal rather than actually measured. Moving to a continuous scale has been suggested to be more sensitive and useful

(Sivkov & Akabaliev, 2003). For this reason, the chapter focused on a quantitative rather than categorical assessment of the common MPA of curvature of the fifth (little) finger as described in chapter 2. This marker has several advantages. It is known to be particularly common among older people. It has also been suggested as an indicator of accumulated stressors, including familial factors, trauma (Flatt, 2005), and a wide range of inflammatory processes (Sokka et al., 2009). As a potential biomarker of aging, it is predicted that greater fifth finger curvature will be associated with greater cognitive decline. Moreover, as it is proposed that finger MPA is a specific biomarker for aging it is also predicted that curvature does not solely arise as a result of specific age-associated pathologies such as arthritis. It is therefore predicted that the association of MPA and cognitive decline should persist even after accounting for the use of anti-inflammatory drugs and levels of C-reactive protein (CRP), indicators of specific illnesses (such as arthritis) that might influence curvature.

7.2 Method

Full details of the sample can be found in chapter 2 section 1.2. Details of the method used to construct the outcome measure can be found in chapter 2 section 1.7.4. As previously, due to completion rates varying across measurements, the values presented here may vary slightly across the empirical chapters featuring this sample.

7.2.1 Participants

Participants were members of the Lothian Birth Cohort 1921 (LBC1921). The initial recruitment and testing of this 550-strong sample has been described elsewhere (Deary, et al., 2004). Participants were all born in 1921 and took part in the Scottish Mental Survey 1932 (SMS) at an average age of 11 years. They were subsequently recruited for further cognitive and medical tests beginning at age 79, in 1999-2001. Measures analysed here were taken at testing waves where the mean age of the participants was about 79 and 87 years.

Of the initial wave of 550 (234 men and 316 women), 454 were contacted for the second wave at age 83 (335 agreed, and 321 were tested, of which 145 were men and 176 were women). Excluding those who had died or withdrawn, 268 were contacted for wave 3 at age 87 and 207 completed all the measures (Starr et al., 2010). The analyses here use data from childhood, and waves 1 and 3. Testing at waves 1 and 3 was conducted at a Clinical Research Facility.

7.2.2 Procedure

7.2.2.1 Cognitive Ability Test

Cognitive ability at mean ages of 11, 79, and 87 years was assessed using the Moray House Test No. 12 (Deary, et al., 2004; Scottish Council for Research in, 1933). This is a 45-minute, time-limited test of verbal (principally), numerical, spatial and abstract reasoning with a maximum possible score of 76. Scores were controlled for age in days at time of testing and then converted to a standardized IQ-type scale (with $M = 100$ and $SD = 15$).

Participants completed the mini-mental state examination (MMSE) at age 87, a screening tool for cognitive impairment (Folstein, Folstein, & McHugh, 1975). The mean score was 27.80 ($SD = 2.22$) out of a maximum total score of 30. This variable was recoded, with scores above 23 indicating normal or near-normal functioning ($n = 182$), and scores at 23 or below indicating possible impairment ($n = 10$).

7.2.2.2 Parental Education

Between ages 80-81, participants answered questions on their family history, including number of years of parental education. Father's education was $M = 10.10$ ($SD = 3.00$), and mother's education was $M = 9.68$ ($SD = 2.36$).

7.2.2.3 Minor Physical Anomalies

At mean age 87 in wave 3, participants undertook a variety of physical and mental tests including having both hands scanned individually using a high-resolution flatbed scanner. In total, 192 participants (90 male, 102 female) completed the hand scan and provided usable images.

Curvature of the fifth digit (the little finger) was assessed using GIMP image editing software (available at www.gimp.org) to record digitally the length and angle of each segment of the

little finger. The change in angle between each segment was summed and averaged bilaterally providing a continuous MPA severity variable. All other studies investigating curvature of the fifth digits have simply categorized the digit as being either very curved, slightly curved, or not curved. The present study is the first in this research area to use a continuous measurement of curvature. To test reliability, fifth digit curvature was measured for three participants drawn from another sample (with no relation to the participants in the present study). Each participant provided two different images of both hands. The intraclass correlation coefficient for each of the three pairs was calculated by comparing the curvature of the fifth digits between the paired images (ICC type 3). Results were $r = 0.89, 0.85$ and 0.90 for the three pairs, indicating very high reliability.

7.2.2.4 Inflammatory Markers

At age 79, use of anti-inflammatory drugs (NSAID) was recorded categorically as either use or non-use according to self-report. This class of drug is most frequently used in older adults to treat pain caused by inflammation. 14 participants reported use of NSAIDs and were removed from the analysis. At mean age 87 in wave 3, levels of CRP were measured via blood test. CRP levels increase significantly during inflammation (from, among other factors, arthritis). Mean CRP level was 3.96 mg/l , $SD = 8.61 \text{ mg/l}$ (median 1.92 mg/l).

7.3 Results

The sample had a mean curvature of 3.83° ($SD 2.26^\circ$). On average, females had around 25% greater curvature ($N = 102$, $M = 4.24^\circ$, $SD = 2.20^\circ$) than males ($N = 90$, $M = 3.37^\circ$, $SD = 2.24^\circ$). This sex difference was significant and of medium effect size ($t(190) = -2.72$, $p = .007$, $d = 0.39$). Curvature in excess of 8° is considered abnormal (Smith, 1970) but few subjects exhibited these levels of curvature. Fig. 7.1 displays an image of, from left to right, low, moderate, and high curvature. When the sample was ranked from lowest to highest, the images were representative of the 25th, 50th, and 75th percentile for curvature. The correlation matrix of all variables is given in table 7.1.

Fig. 7.1 – Low, Medium, and High Curvature of the Fifth Digit



Note: images are representative of the 25th, 50th, and 75th percentile when participants are ranked according to curvature score from lowest to highest.

To ensure comparability with past research this area has reproduced traditional methods – most frequently correlation or regression analysis (see e.g. Rosenberg and Weller (1973). While alternatives – such as multilevel modelling – might be a plausible alternative method they are beyond the scope of the present work. As is common with past work the present work does not initially correct for multiple comparisons – see section 7.3.1 for corrected values.

Three models were tested using multiple linear regressions to assess the association between finger curvature and cognitive change: between age 11 and age 79, between age 11 and age 87, and between age 79 and age 87. The models initially included father's and mother's education, MMSE score and C-reactive protein level as covariates. C-reactive protein level did not influence the models and so was dropped. MMSE score did not influence the significance or magnitude of curvature scores and so was dropped. Father's and mother's education, which correlated highly with age-11 and age-79 IQ and for some analyses approached significance, were retained. The models also initially excluded users of anti-inflammatory drugs, but model fits and significance of the predictors did not vary according to whether they were excluded so were retained in the final models. Results for all three models are presented in table 7.2.

Table 7.1 - Correlation matrix of intelligence, curvature, mini-mental state examination score and inflammation

	Age-11 IQ	Age-79 IQ	Age-87 IQ	Father's Education	Mother's Education	Curvature (right fifth digit)	Curvature (left fifth digit)	Curvature (average of both digits)	Use of anti- inflammatory drugs	C-reactive protein level (age 87)	Mini-Mental State Examination age-87
Age-11 IQ		.659* * (485)	.513** (178)	.139* (338)	.122* (336)	.031 (168)	.111 (168)	.089 (168)	.051 (460)	.116 (161)	.327** (183)
Age-79 IQ			.707** (200)	.154** (377)	.118* (375)	-.073 (189)	-.039 (189)	-.070 (189)	.028 (460)	.078 (182)	.460** (204)
Age-87 IQ				.093 (166)	.082 (166)	-.051 (186)	.020 (186)	-.019 (186)	.028 (173)	.018 (178)	.568** (200)
Father's Education					.744** (374)	-.038 (159)	.216** (159)	.103 (159)	-.018 (322)	-.063 (151)	.146 (169)
Mother's Education						.052 (160)	.032 (160)	.053 (160)	.026 (320)	-.118 (152)	.168* (169)
Curvature (right fifth digit)							.289** (192)	.	-.043 (162)	-.068 (180)	.020 (192)
Curvature (left fifth digit)								.	.049 (162)	.004 (180)	.015 (192)
Curvature (average of both digits)									.005 (162)	-.040 (180)	.022 (192)
Use of anti- inflammatory drugs										.070 (157)	.088 (177)
C-reactive Protein level (age 87)											-.167* (184)

Note: * indicates $p < .05$, ** indicates $p < .01$, *** indicates $p < .001$. Values are correlation coefficient (r) with sample size in brackets. Part-whole correlations for digit curvature not shown.

Table 7.2 - Linear regression models of Moray House Test IQ at age 79 and 87. Effects are given as B (SE), with standardised β below.

	Model 1: IQ change from 11 to 79			Model 2: IQ change from 11 to 87			Model 3: IQ change from 79 to 87		
	All subjects	Males	Females	All subjects	Males	Females	All subjects	Males	Females
Age 11 IQ	.56 (.06)	.56 (.08)	.57 (.09)	.53 (.09)	.52 (.14)	.58 (.11)	.09(.10)	.02(.16)	.18(.12)
	.65***	.68***	.62***	.50***	.49***	.54***	.09	.02	.17
Age 79 IQ							.79 (.11)	.92 (.19)	.70 (.13)
							.11***	.70***	.60***
Father's Education	.25 (.38)	-.06 (.60)	.48 (.51)	.04 (.56)	.41(1.02)	-.36 (.64)	-.13 (.48)	.59 (.86)	-.69 (.54)
	.07	-.02	.13	.01	.08	-.08	-.03	.12	-.16
Mother's Education	.10 (.45)	.41 (.74)	-.08 (.62)	.20 (.69)	-1.09 (1.28)	1.36 (.78)	.08 (.59)	-1.65 (1.08)	1.42 (.65)
	-.18	.09	-.02	.03	-.18	.25	.01	-.27	.26*
Finger curvature	-1.00 (.36)	-.48 (.53)	-1.62 (.54)	-1.28 (.54)	-1.04 (.89)	-2.03 (.68)	-.55 (.47)	-.72 (.75)	-.90(.61)
	-.18**	-.09	-.28**	-.19*	-.15	-.30**	-.08	-.10	-.13
Adjusted R ²	.46	.48	.42	.26	.20	.33	.47	.44	.54

Note. * $p < .05$, ** $p < .01$ *** $p < .001$. Significant values are indicated in bold.

As can be seen from table 7.1, intelligence at 11, 79 and 87 were positively correlated and the effect sizes of these associations were large. Digit curvature, however, did not correlate with the intelligence variables. The models therefore focused on cognitive change.

Model 1 examined predictors of IQ change between age 11 and 79. It used age 79 IQ as the outcome variable, predicted by finger curvature, and with age-11 IQ and father and mother's education as covariates. Including age 11 IQ effectively tested the contribution of finger curvature to the change in IQ between age 11 and age 79. As expected, age 11 IQ made a large and significant contribution to IQ at age 79, so that those with greater IQ at age 11 had greater IQ at age 79. Parental education did not contribute significantly to the model, whereas finger curvature did ($\beta = -.18$ $p = .01$): greater finger curvature was associated significantly with greater relative IQ decline between age 11 and 79. When the sexes were analysed separately, the contribution of finger curvature was significant in women ($\beta = -.28$, $p = .004$), but not in men (though the direction of effect was the same as for women: $\beta = -.09$, $p = .37$). The magnitude of the effect sizes of men and women were compared through converting the coefficients into Fisher's Z scores then testing whether they differed significantly (McGeorge, et al., 1996): the correlations did not differ significantly in size ($p = .18$) and consequently this difference should not be over-interpreted.

Predictors of IQ change between 11 and 87 were examined next (model 2). Age 87 IQ was the outcome variable, with the same covariates as in model 1. As in model 1, age 11 IQ contributed significantly to IQ at age 87 so that those with higher IQ at age 11 had relatively higher IQ at age 87. Finger curvature also accounted for a significant amount of variance in age-87 cognitive decline ($\beta = -.19$, $p = .02$). Sex-specific analyses found finger curvature significant in women ($\beta = -.30$, $p = .004$), but not in men ($\beta = -.15$, $p = .25$). Again, the magnitudes of the two associations did not differ ($p = .28$). In all cases greater curvature was associated with relatively greater cognitive decline.

Model 3 examined change in IQ during old age, from 79 to 87. Age-87 IQ was used as the outcome variable with the same covariates used in model 2 with the addition of age 79 IQ. After accounting for the effect of age 11 IQ, age 79 IQ made a large and significant contribution to IQ at age 87 with higher initial IQ predicting higher IQ at age 87. Finger curvature was not significantly associated with change either in the combined ($\beta = -.08$, $p =$

.24), or sex-specific samples (male $\beta = -.10$, $p = .34$; female $\beta = -.13$, $p = .14$). In women but not men, there was a significant effect of mother's education on cognitive change ($\beta = .26$, $p = .033$).

7.3.1 Statistical Corrections

Applying a Bonferroni correction to the models would have rendered the association between curvature and cognitive ability change from 11 to 87 non-significant for the whole sample. However it would not have influenced the female results which were interpreted as the key area of interest in the main analysis.

7.4 Discussion

A significant association was found between fifth finger curvature and lifetime change in cognitive function after accounting for parental education. The inclusion or exclusion of MMSE scores and signs of inflammation did not influence the findings. Those with higher levels of curvature experienced relatively greater general cognitive decline, scoring lower at both age 79 and 87 than predicted based on their age-11 performances. When the sexes were analysed separately, the results were significant in women but not in men. As such the present study is the first to report an association between a minor physical anomaly and cognitive decline in old age.

Significantly, there was no association between fifth finger curvature and intelligence at age 11. This finding mirrors the results from measures of facial asymmetry and cognitive aging (Penke, et al., 2009), which also revealed links between accumulated asymmetry and cognitive decline, with no relationship to initial levels. This supports the interpretation that greater frequency and severity of minor physical anomalies function as a marker of enhanced cognitive decline, rather than higher initial ability.

The finger curvature MPA has previously been associated with inflammatory processes and stress (Flatt, 2005). The association of this marker with cognitive decline implies that, at least in women, such inflammatory processes may be linked to an increased rate of decline in general cognitive function, relative to baseline levels measured early in life. The present

study provides further support for the idea of a common cause, or set of common causes, as a foundation for the shared variance between cognitive and physical decline (Christensen, et al., 2001).

7.4.1 Findings in the Context of Past Research on MPAs and cognitive ability

The present study also demonstrates further that MPAs are not only indicative of problems in severe cases (e.g., clinically diagnosable conditions such as autism or schizophrenia) but can provide information on behavioural and cognitive variables on a normal continuum. In children, higher levels of MPAs, even when not manifesting in severe developmental disorders, can still predict increased levels of behavioural issues and conduct disorder (Waldrop, et al., 1968). This also seems to be true in male adults, as those men with higher incidences of MPAs demonstrate differences in personality such as emotionality, extraversion, and Type A personality (Paulhus & Martin, 1986). Just as some MPAs are associated with differences in personality traits, they may predict differences in cognitive change over time.

7.4.2 Strengths and Weaknesses of the Study

Among several positive attributes of the present study it is the first to adopt a continuous measure of MPA, allowing a continuous rather than a categorical assessment. The advantage of this is demonstrated by very few of the participants having what would be considered abnormal curvature (Smith, 1970) – using a categorical system only a small number of participants would have demonstrated unusual curvature. Furthermore, in this sample IQ at age 11 was tested rather than estimated ensuring that cognitive change was reliably measured. Similarly, homogeneity of age was a major strength of the present study, largely eliminating the effects of chronological age. The sample was made up of Caucasian Scots, with the professional classes overrepresented as compared to the population. It is unknown how such findings might generalize to other ethnicities and nationalities. However, these factors ensured that subject differences reflected relative differences in biological aging.

While this study is novel in the use of a quantitative measure of an MPA, and draws on an extremely useful longitudinal sample, it is important to note the use of a single MPA is a limitation. Replication and expansion are necessary to better understand the relationship of MPAs to cognitive aging, preferably with additional MPA markers in larger samples to compare the predictive value of multiple morphological traits. Particular attention should be paid to the sex-specificity of MPA effects. In this sample, surviving men showed significantly less curvature, and the cognitive decline-curvature association was significant in women alone, though the direction of the effect was the same in men. Given sex-specific mortality rates, in the present sample males with higher levels of MPA may have incurred increased rates of mortality, reducing the mean level of observed MPA in the remaining population and thus reducing the association with cognitive decline, creating the appearance of sex specificity. Alternatively, the effect may be genuine in both sexes, but not identified here in men due to the relatively smaller sample size. It remains possible that specific MPAs may be more indicative of developmental instability in one sex or the other. Notably, Sokka et al. (2009) found evidence that rheumatoid arthritis was more severe in women as opposed to men. If women are more vulnerable to inflammatory conditions such as arthritis, reduced fifth digit curvature may be indicative of greater developmental stability in women as compared to men. This is uncertain, however, and repeating the study with a broader range of MPAs would be the most effective means of addressing this issue: the fact that the magnitudes of the associations in men and women did not differ significantly means the present findings should be interpreted cautiously and explanations of potential mechanisms should not be overstated.

This concludes the empirical work on cognition and Reaction Times. Intelligence, Reaction Times, and cognitive decline are all linked in some form to symmetry and MPAs. The next chapter focuses on another important topic in symmetry research: personality.

Chapter 8 – Symmetry and Personality

8.1 Introduction

The previous three chapters have demonstrated links between symmetry, minor physical anomalies, and cognitive attributes including intelligence and Reaction Times. The present chapter addresses links between symmetry and an entirely different area of work: that of personality. The focus of this chapter is on expanding the very limited amount of past work described in chapter 1, section 1.8 as a means of evaluating some of the limitations described in chapter 1, section 1.11: especially the limited number of replications in any given area.

Variation in personality is known to be under biological influence and may reflect selective pressures. The nature of these pressures is unclear. By contrast with intelligence, which is believed to be associated with increased fitness (Bates & Shieles, 2003; Furlow, et al., 1997), theories diverge as to the predicted relationships of personality to fitness (see Penke, et al. 2009 and commentaries). Common predictions variously describe high, average, or low levels of each personality trait being adaptive. Alternatively, balancing selection may favour a distribution of phenotypes, none of which have a net relationship to fitness.

One method to test the evolutionary basis of personality is to measure its links to measures of fitness such as developmental stability (Waddington, 1957). Developmental stability reflects the ability to maintain a normal developmental course despite stress (van Valen, 1962). A measure of developmental stability is symmetry (with asymmetry measured as an organism's deviation from bilateral symmetry). Here symmetry is used to test evolutionary models of personality. The chapter briefly review the existing literature, and then describes two new samples including a sample of healthy older adults: a population that has not been studied previously in this field of research.

8.1.1 Personality and Fitness

From an evolutionary perspective, desirable mate characteristics such as low-mutation load and high economic investment, parenting and emotional commitment are ranked most important cross-culturally, and are related to attractiveness (Buss & Shackelford, 2008). This suggests two possible associations between personality and symmetry. First, the big five

personality traits (see e.g. Costa & McCrae, 1992) – Neuroticism (N), Extraversion (E), Openness to Experience (O), Agreeableness (A), and Conscientiousness (C) – may be linearly associated with symmetry, with greater developmental stability promoting, for instance, higher levels of warmth and activity reflected in E.

Extending this argument, some researchers have argued that there is a general factor of personality analogous to the general factor of intelligence and reflecting genetic fitness (Rushton, 1990) though others have argued it is an artefact of certain analytic or methodological strategies rather than a valid construct (see e.g. Just, 2011). If there is a general factor of personality low asymmetry should correlate with high scores on this factor (so an extraverted, open, agreeable, conscientious, emotionally stable individual would exhibit low asymmetry). If there is no association between asymmetry and the general factor it shows either personality is unrelated to asymmetry, or that the general factor is a methodological artefact rather than a meaningful indicator of fitness.

In the strongest case for such links, it has been argued that personality contains a general factor of personality, analogous to the g-factor in intelligence, and which like the g-factor (Bates, 2007; Prokosch, et al., 2005) may reflect genetic fitness (Rushton, 1990). If so, low asymmetry should be associated with high scores on the general factor of personality.

A second promoted fitness link for personality (Gangestad, 2010) suggests that mean trait-levels reflect appropriate development. Under this model, high mutational load (and therefore higher asymmetry) is predicted to be associated with a deviation from the population mean in personality and high asymmetry should be associated with both very low and very high scores on personality traits.

The currently published data address these questions at best partially or, in the case of non-linear models, not at all. To date, only three reports have examined associations between asymmetry and self-reported personality, and none has examined for non-linear associations. Moreover, none has used standard bodily measures of asymmetry. Shackelford and Larsen (1997) examined associations between facial asymmetry and a range of measures in 101 college undergraduates, including Eysenck Personality Questionnaire (EPQ) scales. Asymmetry was positively associated with extraversion in women ($r = .32$), and with neuroticism in men ($r = .49$). By contrast, a similar study of facial asymmetry by Fink,

Neave, Manning, and Grammer (2005) in 120 students given the NEO-FFI (Costa & McCrae, 1992) found that higher facial asymmetry was associated with lower E ($r = -.21$), and higher A ($r = .23$) and O ($r = .30$) scores, with a trend towards higher N ($r = .17$) that was not significant. Finally, Pound, Penton-Voak, and Brown (2007) reported the largest sample to date ($n = 294$), assessing personality with an adjectival rating measure of the big five traits and again assessing facial asymmetry. The sole significant association was for lower E ($r = -.21$). The results to date, then, are at best mixed, with E and asymmetry correlating negatively in two samples (Fink, et al., 2005; Pound, et al., 2007), but in the opposite direction and in women only in another (Shackelford & Larsen, 1997). Similarly N was associated with high asymmetry in men only (Shackelford & Larsen, 1997), and not at all in either the Pound et al. or Fink et al. Studies. Only Fink et al. found significant associations with O or A. Past findings, and their directions, can be found in Table 8.1.

Table 8.1: Summary of Studies Examining Linear Associations of Asymmetry and Personality

Study	Sample Size	E	N	A	C	O
Shackelford and Larsen (1997)	101	.15	.03	-	-	-
Fink et al. (2005)	120	-.21*	.17	.23*	-.07	.31**
Pound et al. (2007)	294	-.21***	.03	-.05	-.01	-.04

*Note: * indicates significance at .05, ** indicates significance at .01, *** indicates significance at .001 (all two-tailed). Shackelford and Larsen measured asymmetry in the face via photographs. They measured asymmetry by establishing bilateral points about a midline drawn through the centre of the face. Fink et al. measured asymmetry in the face via photographs, and established asymmetry through image analysis rather than human measurement. Pound et al. measured asymmetry in the face as symmetry of bilateral points about a midline drawn through the centre of facial photographs. E = Extraversion, N = Neuroticism, C = Conscientiousness, A = Agreeableness, O = Openness to Experience.*

8.1.2. The Present Studies

To expand the available data on symmetry and personality two new samples were collected, assessing standard bodily asymmetry, examining both linear and curvilinear associations between with the big 5 personality traits, as well as the hypothesized general personality factor. The personality inventories used in each study are comparable to each other and inventories used in past research (Gow, Whiteman, Pattie, & Deary, 2005a). All previous samples have been restricted to young samples – here both a young and an old-aged group were used allowing us to examine the generalizability of associations of personality with asymmetry. No studies have tested these relationships among elderly populations, where both asymmetry and personality are known to be in flux (Otremski, Katz, Livshits, & Cohen, 1993; B. W. Roberts & Mroczek, 2008). Furthermore, as at least some personality traits are associated with mortality risk (Kern, et al., 2009), assessing the fitness-relevance of such personality traits in the aged may be particularly important.

8.2 Study 1: Personality and Symmetry in the Lothian Birth Cohort 1921

8.2.1 Participants

Participants were drawn from the Lothian Birth Cohort 1921 (LBC1921). The initial recruitment and testing of this 550-strong sample has been described in detail elsewhere (Deary, et al., 2004): a fuller account can be found in chapter 2 section 2.2.

8.2.2 Personality and Asymmetry assessments

Subjects were assessed on the 50-item version of the International Personality Item Pool (IPIP) Big-Five Factor markers (Gow, Whiteman, Pattie, & Deary, 2005b) at age 81. This test has 10 items for each of the personality traits: extraversion (E), agreeableness (A), conscientiousness (C), emotional stability (ES) and intellect/imagination (O: this abbreviation is used as it is close to the Openness trait of the five factor model). It can be compared to the factors of the NEO-FFI as the correlations between the equivalent traits are high to acceptable (Gow, et al., 2005a).

Asymmetry was assessed at clinic visits at age 87. Due to different completion rates for each measure, participant numbers were as high as 209 for some measures, and 173 participants (80 male, 93 female) completed all measurements. Using digital callipers, ear height, ear width, wrist circumference, elbow circumference, and ankle circumference were measured three times each for the left and right side of the body. Mean values across the three measurements were calculated. Reliability was assessed using the intraclass correlations (ICC type 3) between the three repeated measurements of each body part. Reliability was very high ($r = .998$). All participants had their hands scanned by a digital flatbed scanner, giving high resolution images of the hands. Lengths and widths of the digits (excluding the thumb), along with the lengths of the palms, were measured digitally using image editing software. Where fingers were curved, measurements were taken between each individual joint and then added together, to ensure that finger length was not inappropriately shortened as a result of failing to take account of curvature. Common reasons for exclusion included unacceptable image quality (such as movement during the scan causing distortion) or too few measurements. A subset of 25 images was measured twice by the same rater prior to the rest of the sample being measured. The ICC between the two measurement occasions was again excellent indicating high reliability of the hand asymmetry measure ($r = .999$).

While measurements of the fingers were taken by calliper, high curvature in the fingers of the participants made the callipers less reliable for the fingers than the other body parts. Consequently, the final outcome measure was established by combining the calliper measurements of the body with the digital measurements of the hands. The 14 separate measurements were then combined using the symmetry formula (p21), which is used in most past research (Bates, 2007; Furlow, et al., 1997; Prokosch, et al., 2005) to produce an absolute percentage to create the outcome variable of combined asymmetry. The values were then log transformed for normality.

8.3 Results

Mean asymmetry (before being transformed for normality) was 0.95% ($SD = 0.04$). No significant sex differences in asymmetry were found ($t(171) = -1.31, p = .192$). Linear relationships of asymmetry to each of the 5 personality traits were examined using regression controlling for age and sex (see table 8.2). Of the five tests made, only one personality trait

was nominally significant (O was significantly associated with asymmetry: $\beta = -.16$) in a model which was, overall, non-significant ($F_{3,161} = 1.82$, $p = .15$, adjusted R square = .02). Nonlinear associations of asymmetry and personality were examined as follows. The mean score on each personality dimension was calculated, and the absolute deviation of each participant's score on each domain was calculated. The higher the subsequent deviation score, the further the participant was from the mean – above or below. Using regression controlling for age and sex, no significant associations were found. Full details can be found in table 8.3.

Finally, the hypothesis that asymmetry would relate to a general factor of personality was tested. The first unrotated component of a factor analysis of five personality domains accounted for 38.2% of the total variance in personality and the five factors all loaded significantly onto it (.73, .73, .57, -.43 and .58 for Extraversion, Agreeableness, Conscientiousness, Neuroticism and Openness to Experience respectively). Scores on this first factor were calculated for each participant and the linear and curvilinear regression analyses repeated with scores on this general factor. No significant associations with asymmetry were identified, whether linear or curvilinear (see tables 8.2 and 8.3).

8.3.1 Statistical Corrections

Studies in the area typically do not correct for multiple comparisons (see e.g. Fink et al., 2005). However, after applying a Bonferroni correction no personality trait was significantly associated with asymmetry.

Table 8.2 Linear regression models of asymmetry on personality score, adjusting for age and sex. Numbers are: B (SE), with standardised β below.

	Study 1						Study 2					
	E	N	C	A	O	General Factor	E	N	C	A	O	General Factor
Asymmetry	.13 (1.91)	.45 (2.00)	.41 (1.44)	.28 (1.11)	-2.67 (1.35)	-.09 (.24)	-2.03 (1.68)	1.24 (1.42)	-3.56 (1.62)	-.92 (1.29)	-1.53 (1.84)	-.57 (.29)
	.01	.02	.02	.02	-.16*	-.03	-.08	.06	-.15*	-.05	-.06	-.14
Adjusted R^2	.04	-.02	-.01	.20	.02	.07	.06	.13	.06	-.01	.001	.02

Note. * $p < .05$. Significant values are indicated in bold. E = Extraversion, N = Neuroticism, C = Conscientiousness, A = Agreeableness, O = Openness to Experience.

Table 8.3 Linear regression models of asymmetry on participant's deviation from mean personality score, adjusting for age and sex. Numbers are: B (SE), with standardised β below.

	Study 1						Study 2					
	E	N	C	A	O	General Factor	E	N	C	A	O	General Factor
Asymmetry	.12 (1.19)	-1.78 (1.20)	-.68 (.83)	1.04 (.67)	-.25 (.77)	.13 (.14)	.23 (.98)	-.15 (.89)	-.19 (.97)	1.04 (.74)	-.42 (1.14)	.13 (.18)
	.01	-.12	-.06	.12	-.03	.08	.02	-.01	-.01	.10	-.03	.05
Adjusted R^2	-.01	.003	-.003	-.003	-.02	-.01	-.01	-.01	-.01	.01	-.01	.01

Note. No associations are significant. E = Extraversion, N = Neuroticism, C = Conscientiousness, A = Agreeableness, O = Openness to Experience.

8.4 Study Two: Personality and Symmetry in the Berlin Sample

8.4.1 Participants

Participants were adults recruited from the general population between 20 and 30 years of age (age $M = 23.8$ $SD = 2.9$, $n = 207$). Of these, 92 were male (age $M = 23.8$ $SD = 2.6$) and 115 female (age $M = 23.3$ $SD = 2.8$). For further details of the sample see Penke and Asendorpf (2008) and chapter 2 section 2.5.

8.4.2 Personality and asymmetry assessments

Participants completed the German version of the Big Five Inventory (BFI), details of which are available in Lang, Lüdtkke, and Asendorpf (2001). Participants were measured across 12 body traits using digital callipers: the 2nd, 3rd, 4th and 5th digits along with foot breadth, ankle breadth, knee breadth, hand breadth, wrist breadth, elbow breadth, ear length and ear breadth. Each case was measured twice. If bones were reported as being broken or sprained in the areas of measurement, the participant was excluded. The results of the 12 traits were averaged using the same formula as in study one to create an outcome variable of combined asymmetry. Reliability across the two sets of measurements of each body part, as indicated by the ICC (type 3), was high ($r = .999$).

8.5 Results

Mean asymmetry (before being transformed for normality) was 2.21% ($SD = 0.51$). As in study one, data were log transformed prior to analysis. Male and female asymmetry differed significantly by t-test ($t(205) = -3.28$, $p = .001$, $d = 0.48$) with women exhibiting higher asymmetry.

Again, linear and nonlinear associations with each of the 5 major personality factors and a general factor were examined. Results of tests of linear regression models for each personality trait and asymmetry are shown in table 8.2. Of the five tests conducted, one nominally significant result was found after controlling for age and sex: a negative association of asymmetry and Conscientiousness in a model which was, overall, significant

($F_{3,203} = 5.01$, $p = .002$, adjusted R square = .06). Nonlinear associations were again based on calculated deviations from the mean for each participant. As in study one, no associations approached significance (see table 8.3).

To evaluate the possibility of asymmetry relating to a general personality factor, the same factor analysis was conducted as in Study 1. The first unrotated component accounted for 33.5% of variance in the FFI. The five traits loaded significantly onto the general factor (.78, .35, .53, -.43 and .69 for Extraversion, Agreeableness, Conscientiousness, Neuroticism and Openness to Experience respectively). No significant associations between asymmetry and the general personality factor were found (see tables 8.2 and 8.3).

8.5.1 Statistical Corrections

As in Study 1 statistical corrections were applied to test the effect of multiple comparisons. The single significant uncorrected association (between asymmetry and conscientiousness) would not be significant after applying a Bonferroni correction.

8.6 Joint Discussion of Studies One and Two

In two studies this chapter presented the first examination of personality traits and asymmetry using standard bodily asymmetry measures, and the first data exploring possible links of very high or very low personality scores to asymmetry. The nonlinear associations with personality were perhaps the most interesting and theoretically novel hypotheses examined. Across two studies each examining six possible associations (including associations with the general factor) no support was found for any curvilinear associations between asymmetry and any personality trait. The situation was similar when linear associations were tested: asymmetry was linked to lower O in study one (older subjects), and to lower C in study two (younger subjects). The association between asymmetry and Openness to Experience is in the opposite direction to that reported by Fink, et al. (2005), but in the direction expected given the weak link of Openness to general ability. In summary, in the two studies presented with a total of twenty four associations examined, just two were significant with no repeatability across studies. It seems most likely that two positive results reflect chance.

Taking the present data together with previous studies, it is clear that no personality trait has been reliably associated with asymmetry. Such significant links as have been reported are not consistent across samples. The asymmetry-O and asymmetry-C associations may indicate higher scores on these traits are associated with fitness, but such a proposal is tenuous. Given the reliable association of asymmetry with cognition, and the lack of reliable associations of asymmetry with personality, the present results support models of personality as being unrelated to fitness (Penke, et al., 2007).

8.6.1 Strengths and Weaknesses of the Studies

This chapter described two samples with adequate power. The large number of analyses (and correspondingly small number of positive results, likely indicating false positives) demonstrates that the purported links between asymmetry and personality are not supported or at least not consistently detectable even with adequate power. This study was the first to examine associations between asymmetry and personality in the elderly.

However, the research exhibited some limitations. Notably, the sample age ranges were somewhat restricted. It is possible that, as symmetry varies across the lifecourse (see chapter 4), some life periods may exhibit links between personality and symmetry whereas others do not. Given the previously discussed research on behaviour in children and Minor Physical Anomalies (Waldrop, et al., 1968) this would be a particularly productive area for follow up work.

The present chapter has linked personality to symmetry. It adds to the work of the preceding four chapters and further demonstrates the utility of symmetry research. The next and final empirical chapter examines symmetry in relation to an important measure of wellbeing: socioeconomic status.

Chapter 9 – Symmetry and Socioeconomic Status

9.1 Introduction

The previous five chapters have provided support for links between symmetry and age, symmetry and cognitive ability along with evidence for links between minor physical anomalies and cognitive decline. This chapter examines an important attribute linked to human wellbeing – socioeconomic status (SES) – and its potential links to symmetry. Given the evidence linking symmetry to a variety of important attributes as described in chapter 1 and further supported in the preceding five empirical chapters, it is plausible to expect symmetry to also relate to SES.

9.1.1 Socioeconomic Status: Measurement and Importance

SES—variously assessed using parental income, education, and occupational prestige—is associated with attained status in offspring as well as with their health, morbidity, and longevity (Doyle, et al., 2009; Heckman, 2007). Whereas adoption studies suggest that these cross-generational influences are in part transmitted genetically (Björklund, Jäntti, & Solon, 2007), the early environment might also play an important role. In particular, an influential suggestion has been that the link between early and later life SES lies in dysregulation of basic developmental biological processes such as cellular division, growth and hormonal signalling during foetal and perinatal development. This is predicted to be particularly important for the chronic disease burden associated with SES, including coronary heart disease and type-II diabetes (N. B. Anderson & Armstead, 1995; Barker, 2007). It is further suggested that deprivation-linked dysregulation acts as a signal to the organism to adapt its life history strategy to a shorter, early-reproducing life-cycle. Thus, early events come to programme life history strategy (Barker, 1995, 2007; McMillen & Robinson, 2005). If early life SES exerts its effects on the individual's adult life by disordering the processes of growth (rather than, for instance, by better access to education), then this should be manifested in biomarkers of developmental perturbation such as reduced bodily symmetry, with differences between bilateral body parts reflecting the noise induced in growth by dysregulation of cell-division and other growth-linked processes. Here symmetry is used as a measure of developmental perturbation. This marker is potentially complementary to typical measures

such as blood pressure and obesity, as it has a very early developmental presence and is not itself an explicit disease process. The present study tests associations between bodily and facial symmetry and SES, contrasting symmetry's links with childhood SES and SES attained in midlife.

In the previous chapters and in prior work on the Lothian Birth Cohort 1921, associations have been identified between lower bodily symmetry and lower intelligence, and lower facial symmetry and greater age-related cognitive decline, with effect sizes (r) of around .2 (Bates, 2007; Bates, et al., submitted for publication; Penke, et al., 2009). Whereas bodily symmetry assessed in old age is associated with cognitive ability across the lifespan, facial symmetry measured in old age is associated, in men, not with childhood IQ but rather with relative rate of cognitive decline (Penke, et al., 2009). Thus facial symmetry appears to 'record' stress related to differential aging, and to retain this record into old age. Bodily symmetry is not associated reliably with SES-like variables. Two earlier studies of bodily symmetry report that stressful environments are associated with higher, rather than lower symmetry (Flinn, et al., 1999; Little, Buschang, & Malina, 2002), with other studies finding the reverse outcome (Knierim, et al., 2007). The two markers (bodily and facial symmetry) therefore appear to reflect different sources of perturbations, with facial symmetry providing an effective record of early life disturbances. Consequently, this chapter will focus on associations between facial symmetry and SES. However, it remains unclear which environmental influences cause perturbations and which do not. It is also not logically necessary that exposure to disturbances at one point in time should be more important than disturbances at another point in time, and understanding the time course and action of developmental perturbation is an important goal and may inform policy where it is concerned with the relationship between social status and health. For instance, clarifying the extent to which relatively greater investment might be made in interventions in early life rather than adulthood to ameliorate SES inequalities may aid the optimal expenditure of public funds (Doyle, et al., 2009).

9.1.2 Prior Empirical Work

One recent study has identified a link between facial symmetry and SES. Özener and Fink (2010) examined facial symmetry in Turkish students aged 17-18 years and living in either a wealthy urban area, or a slum district. These authors found significantly lower facial

symmetry in slum compared to wealthy dwelling adolescents. This supports the idea that SES differences may be reflected in facial symmetry. However, it is not clear whether these symmetry differences endure into old age, whether the effects of SES are restricted to the pre-adolescent period, or also reflect SES effects incurred in adulthood.

This chapter examines an elderly sample with measures of both childhood SES and attained occupational social status at midlife, and for whom symmetry of the face and the body were measured in old age. If stress in early development or early life is a substantial contributor to developmental disturbance, an association of symmetry with early life SES is expected. If symmetry largely reflects the total accumulation of stress, then associations between symmetry and later-life challenges, as indexed by mid life attained SES should also be expected. Finally, adult SES may mediate the effects of early life SES on symmetry. Based on recent findings as described in chapter 4, it is predicted that the early life period has a unique impact on developmental stability and, as such, early life SES should be especially associated with symmetry. A structural equation modelling approach was used to test these three hypotheses formally. Given the evidence of sex differences in associations between symmetry and cognitive decline previously identified in this sample (Penke, et al., 2009), males and females were modelled separately. The main focus with respect to associations with SES is on facial asymmetry.

9.2 Method

9.2.1 Participants

Participants were members of the Lothian Birth Cohort 1921 (LBC1921), an originally 550-strong sample whose initial recruitment and testing is fully described elsewhere (Deary, et al., 2004). All participants were born in 1921 and took an intelligence test in the Scottish Mental Survey 1932 (SMS1932) at, on average, age 11 years. They were recruited for cognitive and medical tests in three waves of testing in old age. They were interviewed and tested first in wave 1 of the LBC1921 study at around age 79 years ($M = 79.2$, $SD = 0.6$) between 1999 and 2001. Facial asymmetry measures were collected in wave 2 at around age 83 ($M = 83.4$, $SD = 0.5$). Bodily asymmetry measures were collected in wave 3 at around age 87 ($M = 86.7$, $SD = 0.4$) in wave 3. These ages shall be referred to as 79, 83, and 87 hereinafter.

Of the initial 550 participants (234 male, 316 female), 454 were approached for wave two (335 agreed and 321 were tested, of which 145 were male and 176 female). Removing those who had died or withdrawn, 268 participants were contacted for wave 3, of whom 207 completed all measures, and 237 (109 male, 128 female) completed the questionnaires only (Deary, et al., 2004; Gow, et al., 2011; Starr, et al., 2010).

9.2.2 Procedure

9.2.2.1 Childhood Socioeconomic Status

Between age 80-81 years, participants were sent a self-report questionnaire that asked a series of questions on their socioeconomic status at the time of the SMS1932; in other words, their family SES at age 11. The variables used here included: crowding (measured as number of people per available room, excluding hallways and also toilets which were counted separately); presence of an indoor vs. outdoor toilet (indoor toilet scored as better SES); and the occupational class of the father and mother (coded as I (professional), II (intermediate), III (skilled), IV (semi-skilled), and V (unskilled)). Where the mother never worked occupational class was coded as V (unskilled). Participants also recorded their own highest attained job (in the case of women this could be reported as their highest attained job or the highest attained job of their husband, whichever was higher), and this was classified according to the General Register's Office Census 1951 Classification of Occupations: for full details see Johnson, Brett, and Deary, (2010). This formed the measure of attained class. Details of the relative proportions of each class along with a summary of occupants in the home, relative crowding and toilet facilities by father's social class when the participant was aged 11 are shown in table 9.1. It should be noted that, whereas occupation, toilet facilities, and income do not explicitly include evolutionarily relevant stresses such as food deprivation and parasite burden, they correlate with the likelihood of these events and mortality risk in adulthood (Davey Smith, Hart, Blane, & Hole, 1998). Poor early life SES, but not poor mid life SES, increases the risk of death by stroke and stomach cancer in men (Davey Smith, et al., 1998).

Details of smoking behaviour were examined, but only one participant was an active smoker and the majority of ex-smokers ceased smoking 20 or more years before the late life

measures were taken. Consequently smoking habits were not examined further in the present study.

Table 9.1: Social Class (from childhood and participant's attained mid-life social class), crowding, number of occupants per household and access to toilet facilities.

Social Class	Percentage of each class by			Mean (and SD) of Crowding and Toilet facilities by father's social class		
	Parent		Participant	Number of occupants	Crowding	Access to an indoor toilet
	Father	Mother	Mid-life			
I	8.56%	0%	22.26%	5.67 (2.14)	0.94 (0.63)	100
II	29.45%	18.83%	33.90%	5.11 (1.67)	1.12 (0.64)	88.37
III	47.60%	47.60%	40.07%	5.26 (2.02)	1.86 (1.08)	78.42
IV	9.94%	24.32%	2.05%	5.04 (1.60)	1.97 (1.14)	72.41
V	4.45%	9.25%	1.72%	5.50 (1.51)	2.88 (1.68)	61.54
Total	100%	100%	100%	5.36 (1.85)	1.62 (1.08)	81.85

Note: Total n for each variable = 292. For father, mother and mid-life attained social class, class "I" indicates the highest (professional) quintile, and class "V" the lowest (unskilled labour). Father and mother social class refers to classification of each parent when participants were aged 11. Mid-life attained social class refers to the highest occupational class attained by the participant before retirement. For all subsequent columns, data are subdivided according to father's social when the participant was aged 11. Number of occupants indicates the raw number of individuals in the same house (with SD in brackets). Crowding reflects mean (and SD) of crowding (higher scores are worse - indicating more people per room). Access to an indoor toilet gives the percentage of participants with/without access to an indoor toilet for each social class band.

9.2.2.2 Asymmetry measures

Facial photographs were taken for each participant in wave 2 of the LBC1921 at age 83 years. These were used to calculate horizontal facial asymmetry or HFA – the most common and best-validated measure in facial symmetry research: Grammer and Thornhill, (1994), and total facial asymmetry or TFA – comprising horizontal asymmetry and additional non-horizontal indicators of asymmetry. Full details of the procedure are described elsewhere (Penke, et al., 2009) and are based on established methods (Simmons, et al., 2004). For ease of understanding a slightly different terminology has been used compared to that of Penke et al. and Simmons et al. but the method is the same and is described fully in chapter 1 section 2.2.2. Briefly, photographs were taken under consistent lighting and distance conditions and with subjects holding a neutral expression. 15 bilateral pairs of facial features were subsequently identified, with horizontal asymmetry determined relative to a central midline, and vertical asymmetry relative to the horizontal plane. Asymmetry was calculated using the symmetry formula (p21). A score of zero would indicate perfect symmetry. The greater the score on this variable, the lower symmetry is. Because faces, unlike many other body parts, tend to show directional asymmetry (a mean left-right difference significantly different from zero, indicating that the normal developmental target is asymmetrical, rather than symmetrical), this procedure subsequently identified asymmetry about directional asymmetry using principal components analysis (Penke, et al., 2009; Simmons, et al., 2004). The first two unrotated components of this analysis reflect directional asymmetry and non-directional asymmetry, respectively. Factor scores on the second unrotated component were used in all analyses, thus removing the directional confound (Graham, et al., 1998).

Bodily symmetry was measured at a later clinic visit—wave 3 of the LBC1921 study—at mean age 87 years. Completion rates for each measure varied: 173 participants (80 male, 93 female) completed all measurements. Using digital callipers accurate to 0.1 mm, the following traits were measured: ear height, ear width, wrist circumference, elbow circumference, and ankle circumference on both the left and right side of the body. Each pair was measured three times, and the final score for each trait was the mean across the three measurements. Hand symmetry was assessed using digital flatbed scanning. The lengths of each digit (excluding the thumb) along with their width at the first metacarpal and the breadth

of the palm were measured using digital imaging software (GIMP, available at www.gimp.org). Asymmetry was assessed by summing the 14 measures (5 physical (non-hand based), 9 digital) using the formula displayed above with 0 again indicating perfect bilateral symmetry and higher scores indicating lower symmetry (higher asymmetry). Asymmetry was log-transformed to a normal distribution. Reliability of the calliper measures was examined using intraclass correlations (ICC type 3) between the repeated measurements, and this showed very high reliability (average $r = .998$). Likewise, for the scan data, ICC was computed on a subset of 25 subjects who were scored twice. ICC averaged across the nine measures was $r = .999$, indicating that the measurements taken from each image were highly reliable. Reproducibility was also examined by conducting two separate scans for three individuals not drawn from this sample and calculating the ICC between each pair of images. Results were (r) .993, .989 and .991, further indicating reliability of the measurement process. By contrast with facial symmetry, bodily symmetry typically demonstrates no directional asymmetry (Furlow, et al., 1997).

9.2.3 Statistical analysis

Structural equation models were tested using AMOS version 18 (SPSS Inc, 2010), with full information maximum likelihood (FIML) estimation to maximise information in the presence of missing data. Childhood deprivation was modelled as a single latent variable from the manifest variables of maternal and paternal social class, crowding of the dwelling, and access to an indoor (vs. outdoor) toilet. The homoscedasticity of the relationship between the latent SES trait and both HFA and TFA was evaluated via scatterplots and non-constant variance score tests. For HFA and TFA the non-constant variance score tests returned null results ($\chi^2 = 3.4$, $df=1$, $p = 0.06$ and $\chi^2 = 2.97$, $df = 1$, $p = 0.09$ respectively). For clarity, the scores for the latent trait were reversed so that better (i.e., more favourable outcomes) was scored higher, with lower scores indicating the more adverse outcome.

In all models there was a path between this latent trait of childhood deprivation and mid life occupational social class (also reversed so that higher scores indicated the more favourable outcome). Based on past literature, two plausible pathways were examined from childhood deprivation to facial symmetry at age 83 and bodily symmetry at age 87. The first was a direct path between early life deprivation and late-life symmetry. The second path was

indirect, in which the effect of early life deprivation was mediated via mid life social class to late-life symmetry.

These predictions concerning the associations between childhood and adult SES and symmetry in old age were examined using three models (fig. 9.1). Model 1 tested the effect of both childhood deprivation and mid life occupational social class on symmetry, with direct and indirect (mediated via mid life social class) childhood deprivation effects on symmetry. Model 2 tested the effect of childhood deprivation on symmetry when the effect of mid life social class on symmetry was constrained to 0. Model 3 examined the effects of mid life social class on symmetry when the direct effect of childhood deprivation on symmetry was constrained to zero.

The goodness of fit statistics used were Root Mean Square Error of Approximation (RMSEA), chi-square, and comparative fit indices including the Normed Fit Index (NFI), Tucker-Lewis Index (TLI), comparative fit index (CFI) and Akaike Information Criterion (AIC). The models examined whether HFA, TFA, or bodily asymmetry showed associations with childhood deprivation or mid life social attainment.

9.3 Results

Table 9.2 shows the bivariate correlations of the four markers of deprivation as well as facial and bodily asymmetry calculated using both pair-wise and list-wise deletion. Magnitudes of the correlations were similar for each method. The four deprivation indicators correlated significantly, between .19 and .42 (mean = .28). Facial and bodily asymmetries were not significantly correlated, and no asymmetry indicator was associated significantly with any individual SES indicator. Means and SDs for all manifest variables are shown in the bottom row.

Table 9.2: Correlation Matrix of Deprivation and Asymmetry variables

	SES of Father	SES of Mother	Occup/ per house	Crowding Index	Indoor toilet (yes/no)	Mid-Life SES	TFA	HFA	Bodily Asymm.
SES of Father	-	.285	-.096	.450	.220	.238	-.016	-.190	.011
SES of Mother	.310	-	-.213	.180	.200	.388	.011	-.075	-.069
Occup/ per house	-.020	-.042	-	-.054	-.022	-.038	-.098	-.023	.131
Crowding Index	.416	.204	.039	-	.479	.372	.041	-.039	.017
Indoor toilet (yes/no)	.220	.188	.039	.318	-	.179	-.036	-.060	-.024
Mid-Life SES	.257	.251	.037	.332	.157		-.010	-.123	.075
TFA	-.099	-.158	-.035	-.114	-.106	-.085		-	.125
HFA	-.169	-.165	-.019	-.112	-.130	-.088	-		.124
Bodily Asymm.	.044	-.015	.148	.028	.056	.052	.124	.124	
Mean	2.720	3.240	5.360	1.622	1.181	2.270	-.034	-.017	-4.737
(SD)	(.917)	(.864)	(1.85)	(1.083)	(.386)	(.888)	(1.073)	(.997)	(.314)

Note: Bold figures indicate statistically significant correlations. Correlations below the diagonal use pair-wise deletion. Correlations above use list-wise deletion. For pair wise deletion n ranged between

76 and 292. For list-wise deletion, $N = 76$ for all values. Note: low n (76) occurs due to relatively fewer cases providing data on bodily asymmetry. As HFA is a subcomponent of TFA, correlations between the two are not shown here. SES = Socioeconomic Status as indexed by Social Class. Occup/ per house = Number of occupants per household. Bodily Asymm. = Bodily Asymmetry. SES of Father, SES of Mother, Number of occupants per household, crowding index, and indoor toilet variables are given for when the participant was aged 11. TFA = Total Facial Asymmetry. HFA = Horizontal Facial Asymmetry.

9.3.1 Model fitting

The correlations between the SES indicators and the symmetry measures were all non-significant. However, there is an intrinsic benefit of latent variable analysis in aggregating weak signals, which is what the individual indicators provide. This aggregate is more useful than any single indicator. Models of the associations between early life SES and mid life status and old-age symmetry were tested separately using bodily asymmetry, HFA, and TFA. Because only facial (as opposed to bodily) asymmetry is associated with lifetime cognitive decline (Penke, et al., 2009), and bodily asymmetry is inconsistently associated with deprivation (Flinn, et al., 1999; Knierim, et al., 2007; Little, et al., 2002) bodily asymmetry was not expected to be sensitive to SES in this sample, but it was expected that there would be significant associations between SES and facial asymmetry. The data confirmed these expectations of differential associations of bodily and facial asymmetry with SES: Models including bodily asymmetry showed no significant associations with SES in childhood ($p = .79$) or adult attained SES ($p = .77$). Because bodily asymmetry was not significantly associated with deprivation, it will not be discussed further. For facial asymmetry, relationships with deprivation were strongest for HFA, as compared with TFA. For the initial modelling of the full sample models focused on HFA due to its better established validity, and then reproduced analyses for both HFA and TFA for the sex specific analyses.

Fig. 9.1 provides a visual comparison of the three models in which childhood and adult SES are associated with HFA. Model 1 incorporated a latent-trait model of deprivation based on the four markers of childhood status, and related this to the person's own mid life occupational social class and also included direct and indirect (mediated via mid life social class) pathways of childhood SES effects on HFA. It fit the data well. Each of the four indicator variables loaded on to the latent trait of childhood deprivation significantly. The childhood deprivation latent trait was associated significantly with mid life occupational

social attainment (standardised path coefficient = .47, $p = .001$). The direct path from childhood deprivation to HFA was significant and in the predicted direction ($-.28$, $p = .04$); more deprived children had less symmetrical faces in old age. The path from mid life social class to HFA was near to zero ($.04$, $p = .70$). In Model 2, this path was dropped and this did not reduce fit significantly by comparison with Model 1 ($\chi^2(1) = 0.14$, $p = \text{ns}$). Details of model fit statistics are shown in table 9.3. The effect of childhood deprivation on HFA remained significant and similar in magnitude to the parameter obtained in Model 1 ($-.24$, $p = .04$). By contrast, Model 3, in which the path from childhood deprivation to HFA was dropped, fitted significantly less well than Model 1 ($\chi^2(1) = 4.25$, $p = <.05$). Based on both comparative fit indices and χ^2 results, Model 2 was accepted as providing the best fit to the data, indicating that childhood deprivation is directly associated with asymmetry in old age, and that the effect is not mediated by mid life social class. Mid life occupational social class itself had no significant association with asymmetry.

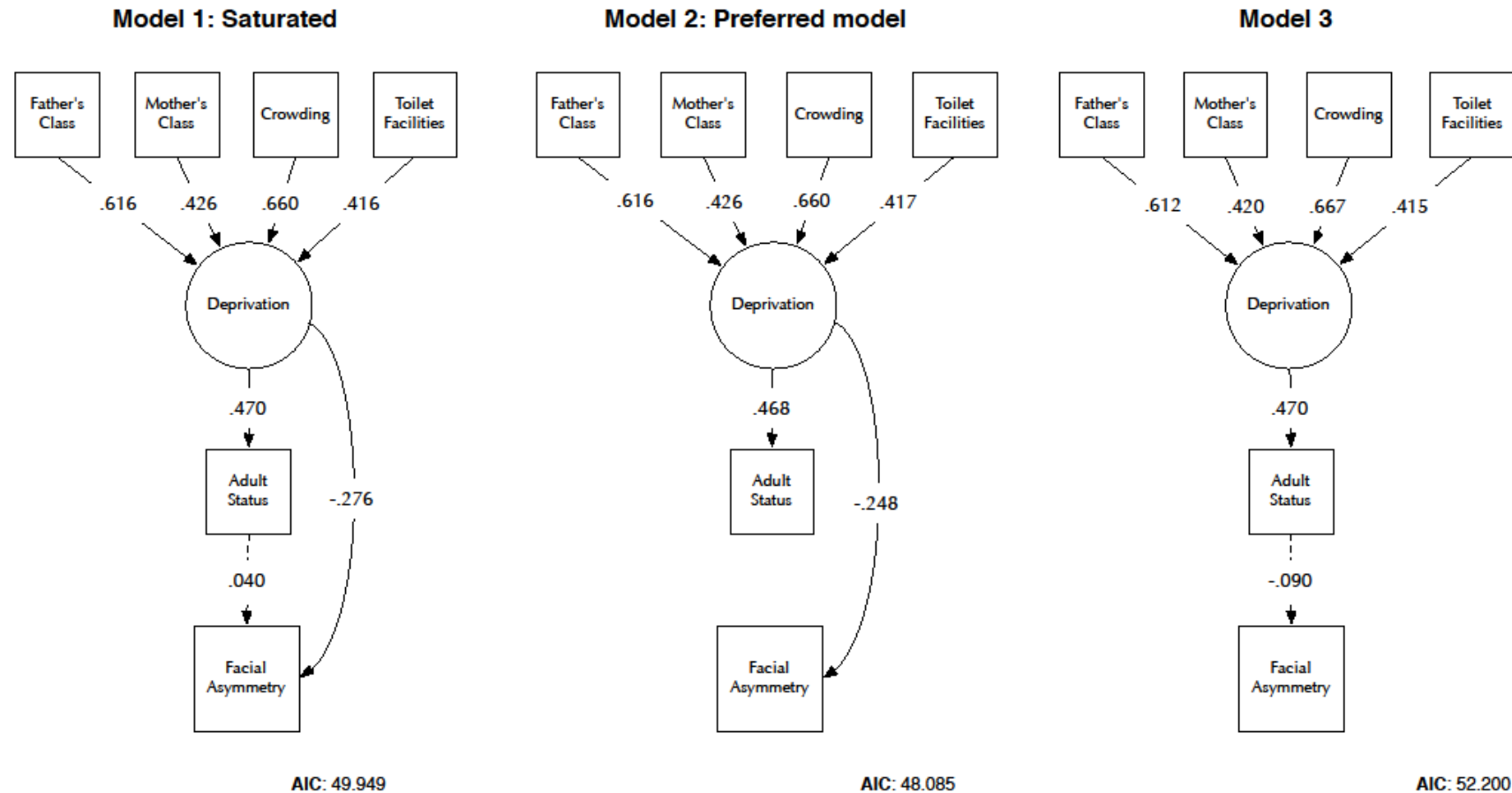
In prior research in the same sample (Penke, et al., 2009), analyses of sex differences in facial asymmetry associations yielded significant results for men but not women. Consequently, Model 2 was rerun separately for men and women. In women there was no significant association between early life deprivation and either HFA ($-.12$, $p = .37$) or TFA ($-.09$, $p = .52$) and models for women are not discussed further. For men, details of model fit statistics are shown in table 9.3. A visual representation of the two models in men is shown in fig. 9.2. In men, the association between early life deprivation and HFA (Model 2b: $-.44$, $p = .03$) and early life deprivation and TFA (Model 2c: $-.40$, $p = .04$) were both significant. The magnitude of the effect sizes for males and females were compared by turning the two coefficients into Fisher's Z scores and testing whether the two differed significantly. For further details see McGeorge, Crawford, and Kelly (1996). For both HFA and TFA males exhibited a statistically significantly stronger relationship ($p = .004$ and $p = .006$, respectively).

Table 9.3: Measures of Statistical Fit for Models Relating Early– and Mid-life Social status to Horizontal and Total Asymmetry at age 87 (see text and fig. 9.1 and 9.2)

	Model 1	Model 2	Model 3	Model 2b	Model 2c
RMSEA	.041	.034	.052	.064	.074
NFI	.933	.933	.910	.780	.756
TLI	.935	.955	.894	.745	.659
χ^2	11.949	12.085	16.200	13.301	14.787
CFI	.975	.981	.955	.890	.854
AIC	49.949	48.085	52.200	49.301	50.787

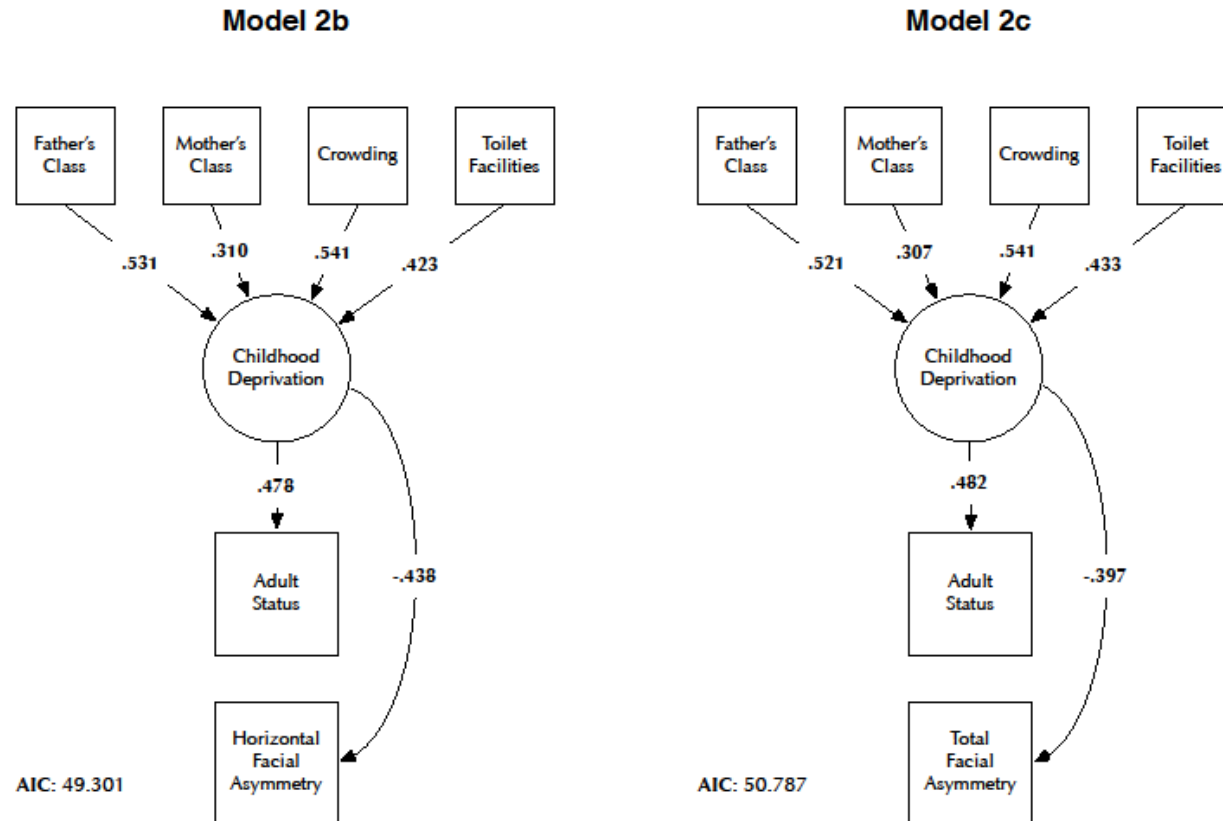
Note: χ^2 difference test was significant for the comparison of Models 1 and 3, but not between Models 1 and 2. RMSEA = Root Mean Square Error of Approximation, NFI = Normed Fit Index, TLI = Tucker-Lewis Index, CFI = Comparative Fit Index, AIC = Akaike Information Criterion. Model 1 examined Horizontal Facial Asymmetry (HFA) with no paths constrained to 0. Model 2 repeated model 1 but with the path between adult status and HFA constrained to 0. Model 3 repeated model 1 but with the path between childhood deprivation and HFA constrained to 0. Model 2b tested model 2 using the same variables but included only men. Model 2c tested model 2 using the same variables except for Horizontal Asymmetry (HFA) which was replaced by Total Facial Asymmetry (TFA), and, like model 2b, included only men.

Fig. 9.1: Models relating Early- and Mid-life Social status to Horizontal Facial Asymmetry at age 87, men and women combined (see text for explanation and table 9.3 for fit statistics)



Note: The latent trait (deprivation) is represented as a circle, and manifest variables as rectangles. Dashed lines indicate non-significant paths. Paths constrained to 0 are not shown. For ease of understanding scores for the latent trait of childhood deprivation and scores for adult status have been reversed so that higher scores indicate a better (more favourable) outcome.

Fig. 9.2: Models relating early- and midlife social status to Horizontal and Total Facial Asymmetry at age 87 in men only (see text for explanation and table 9.3 for fit statistics)



Note: The latent trait (deprivation) is represented as a circle, and manifest variables as rectangles. Paths constrained to 0 are not shown. For ease of understanding scores for the latent trait of childhood deprivation and scores for adult status have been reversed so that higher scores indicate a better (more favourable) outcome.

9.4 Discussion

The results show a significant association between early life deprivation and facial (but not bodily) symmetry: those who experienced better early life SES had higher late life facial symmetry. The association is stronger among men, and non-significant in women. This reinforces the value of facial symmetry as a sensitive marker of developmental perturbation and suggests possible mechanisms by which SES comes to be associated with health and capability. Such mechanisms may include the level of nutrition during childhood, quality of treatment of illness, or parental behaviour in regard to smoking and/or alcohol consumption.

This research indicated distinct associations with SES for measures of bodily symmetry and facial symmetry. No single SES component was significantly related to symmetry, but all components loaded the latent trait of SES heavily, and this trait was linked to symmetry. This highlights both the value of latent trait modelling (J. C. Anderson & Gerbing, 1988) and the multidimensional nature of what is commonly viewed as “capability” (Alkire, 2008; Sen, 1999): as capability is indicated by many different variables, more accurate results will be achieved through maximizing the number of indicators. Individual differences in these two forms of asymmetry appear to capture distinct developmental processes and they are known to have different associations with lifespan intelligence. Prior work has suggested that bodily symmetry reflects the precision of molecular assembly and three-dimensional morphology (Bates, et al., submitted for publication). By contrast, the arguably mostly soft-tissue symmetry indexed by facial symmetry appears more sensitive to environmental impacts and is linked to differential rates of decline in old age, rather than to more stable trait levels of ability (Penke, et al., 2009). Also included in these mechanisms may be parental behaviours such as alcohol consumption, improper treatment of childhood illnesses, suboptimal provision of nutrition during child development, presence of toxins in the childhood environment, and/or smoking during pregnancy. Overall, the accumulating findings in this field of research support the possibility those bodily and facial symmetries are sensitive to different influences; consequently, they should not be treated as interchangeable.

As predicted from statistical links of early development with health (Marmot, 2010) and hypotheses within a developmental origins framework (Barker, 2007), the effects of childhood deprivation were enduring: they remained detectable in facial symmetry measured,

in this case, over 70 years later. The specificity of this association for early life SES rather than for self-attained mid life status (despite the latter being closer in time to the symmetry measure) further supports the hypothesis that childhood is a sensitive developmental period. While the present results suggest that facial symmetry signals environmental factors rather than genome-wide fitness, the genetic and/or epigenetic factors in facial symmetry should be elucidated further. Recent evidence that the ability to generate alternative phenotypes (based on epigenetic modification) may aid an organism under stress and decrease immediate disease susceptibility at the cost of lower fitness later in life (Feinberg and Irizarry, 2010; Frisanco, 2009) may be relevant. Taking these findings into account, it is possible that facial symmetry reflects an interaction of stress with genetic responsivity to stress.

The present study has some limitations. The findings suggest that facial symmetry, with its tight connections to early life development and the laying down of a symmetrical body plan, encapsulates processes which are complete prior to mid life, though they will go on to influence successful aging. The early life latent trait of deprivation, however, captured factors not included in the single-indicator mid life occupational status attainment measure (e.g., crowding and accessibility of toilet facilities). Had these measures been available in mid life, it is possible that they might have shown association to on-going influences on facial symmetry. In addition, data was available only for social factors in early life: biological measures of early development such as birth complications should be sought which may tap additional factors in early development. In particular it would be of value to capture direct markers of foetal development and relate these to symmetry. Furthermore, whereas the age of the participants is advantageous in capturing a lifetime of SES effects, the sample experienced a relatively affluent mid life and has lived approximately two and a half decades beyond the life expectancy of their birth cohort by the time facial measurements were taken (General Register Office for Scotland, 2010). As a side finding, these data also show substantial class mobility in 1930's Scotland, with a more than doubling of persons in class I at middle age relative to their own parents' early life. This is part of a well-known absolute upward mobility trend as a result of changes in the structure of available jobs. For more details about class mobility in this sample see Johnson, Brett, and Deary (2010).

A limitation of the study is that members of the cohort who experienced deprivation in mid life were less likely to reach old age or were less likely to participate in this research.

However, this range restriction would be expected to lead to an under-estimate of the association of early life SES with mid life SES, as those with the worst deprivation and ill health would be more likely to die younger and less likely to respond to a research recruitment advertisement: see e.g. Marmot (2010) and Nishiwaki, Clark, Morton, and Leon (2005) respectively. Associations between deprivation and health are not restricted to the most deprived, but are present across the social spectrum (Marmot, 2010).

Importantly, the findings are significant in the overall sample, but sex-specific analyses indicate that significant results only emerge in men. Males exhibited a statistically significantly stronger association than women between poorer early life SES and lower late life facial symmetry. Further research with larger samples will be required to investigate whether a smaller, though still significant, association exists in women. The sample was drawn from a period where female employment – especially in more professional roles – was comparatively unusual, and mid life female attained status was recorded as either their own status, or that of their husband. Consequently, it is possible that the measures of SES in mid life were less relevant for females than for males. Alternatively, women may be more resistant to environmental stress. In prior research in the same sample (Penke, et al., 2009) associations between symmetry and cognitive ability were significant for men only. It is possible that males exhibit greater associations between symmetry and a wide range of attributes due to sex differences related to the tradeoffs between bodily maintenance and reproductive success. Further research measuring female self-attributed SES would be helpful in identifying which of these hypotheses is correct.

The data support associations of SES with markers of development in early life in the form of facial symmetry, with men who experience relatively better early life SES exhibiting higher facial symmetry in late life.

This concludes the empirical section of the thesis. The next chapter discusses the empirical findings, limitations, and conclusions derived from the empirical work. Finally, it addresses the outstanding issues not addressed by the present studies.

Chapter 10 – Discussion

This chapter reviews the empirical findings chapter by chapter and demonstrates how each contributes to our understanding of symmetry and how it associates with the variables tested in chapters 4-9. The chapter will also show how the new findings can be incorporated into the existing literature and how they have advanced the area. Limitations in the present work, and potential for future work, are also addressed.

10.1 Results

The findings collectively support the proposition that symmetry indicates the overall well-functioning of the organism as first proposed by Van Valen (1962). In the present work asymmetry of the face and the body (internal and external) has been linked to wellbeing. As asymmetry has been shown to vary across the lifecourse (see chapters 4 and 5), the proposition that symmetry is indexing overall wellbeing is plausible. For example, the optimization and subsequent decline in symmetry reflects the trend in cognitive ability (Craik and Bialystok, 2006). Such a trend cannot be explained by symmetry being a byproduct of other variables, so the proposal that direct effects of asymmetry are important is unsupported (van Dongen, 2011). High asymmetry has been linked in the present work to growth periods in children, lower intelligence, slower Reaction Times (RTs), and Socioeconomic Status (SES). As predicted from theoretical work on personality and fitness (Penke, et al., 2007), no association was found between asymmetry and personality (see chapter 8). In one further chapter, a variable related to symmetry (minor physical anomalies or MPAs) was linked to cognitive decline. The following sections will briefly reiterate the findings with effect sizes where appropriate, and how these findings contribute to the literature as discussed in chapter 1

10.1.1 Asymmetry Scores

As discussed in chapter 1, section 1.2, there is little agreement on the expected mean level or variability of asymmetry within humans. Although some authors have suggested mean

asymmetry scores tend to be around 1% or less (Lens, et al., 2002) there has been little systematic work on the topic. Given the different traits used, it is uncertain how comparable different measures are when scoring asymmetry. Of the four samples described here, none exhibited an unusually high level of asymmetry by these standards, though notably the lowest level of asymmetry (sample mean = 0.52%) was observed for the endogenous bone measures. A comparison of mean or variability of asymmetry scores across samples was not the goal of the present work so the topic is not discussed in detail. The scores do, however, support the findings of Lens et al. Samples with asymmetry scores in excess of 1% do not appear common, so cases where they occur may be evidence of an unusually stressed sample or possibly high measurement error.

10.1.2 Symmetry across the lifecourse

There is a significant nonlinear association between age and asymmetry in the Science Festival Sample (SFS). This matches the pattern of growth in children and appears to indicate that, as children approach maturation asymmetry declines. This decline is interrupted by a flat period during which the child grows rapidly. The effect size was relatively small ($\beta = -.162$).

The present study is therefore the first replication of the finding of Wilson and Manning (1996). As discussed in chapter 1 section 1.6, despite the well known tendency for cognitive attributes to improve during childhood and decline in old age (Craik & Bialystok, 2006) no other work has been published on the topic. Although, as shown in chapter 4, such a trend supports the proposition that asymmetry is providing important information about overall integrity, the important finding of Wilson and Manning had not previously been replicated. The present work provides increased confidence in Wilson and Manning's findings and reiterates the importance of accounting for participant's age when conducting research on symmetry.

Added to this, while it was not the main focus of the study, asymmetry was linearly associated with age in the Orkney Complex Disease Study (ORCADES). As described in chapter 5, older participants exhibited significantly higher asymmetry ($r = .15$). This reinforces the findings of Kobylansky and Livshits (1989) who also identified a linear increase in asymmetry with age. Models should account for age wherever possible, and

comparisons of samples with very different mean ages should take this variable into account where findings differ.

10.1.3 Symmetry and Intelligence

Symmetry is related to intelligence. In the ORCADES intelligence was linearly associated with lower asymmetry ($\beta = -.11$) but after accounting for the covariates of age, birth weight, and the experience of bone breakage, this was significant in men ($\beta = -.24$) but not women ($\beta = -.02$). The effect sizes differed significantly between the sexes.

These findings agree with those of the recent meta-analysis on asymmetry and intelligence (Banks, et al., 2010), which was published while the present work was in progress. As discussed in chapter 1 section 1.7, several outstanding issues in the field of asymmetry and intelligence research were not addressed by the literature discussed in the Banks et al. meta-analysis. These included low sample sizes, a tendency to not account for potentially important covariates, and a lack of attention to sex differences. The empirical work described in chapter 5 addressed these issues directly. The large sample size, the inclusion of potential confounds such as age, birth weight and the experience of broken bones, along with the examination of sex differences considerably expands upon the existing work in the field. The final model included 491 participants, whereas the average sample size of the published studies described by Banks et al. was only 134. The large replication demonstrates confidence in the original findings, and supports the caution urged in the Banks et al. paper with regards to effect sizes. While some authors (Thoma, et al., 2006) have reported effect sizes (r) of close to $-.50$, both the meta-analysis and the present work suggests this may be due to low sample sizes and publication bias, and the actual effects are smaller than this. As such the present work contributes to both increased confidence in past work and clarification of the likely size of the relationship.

In addition, the work in chapter 5 usefully addressed the issue of covariates and the lack of attention to sex differences. As described above, the covariates operated differently according to sex (older women, but not older men, were significantly more asymmetrical, and the effect sizes were significantly different in magnitude). This suggests that different variables may

influence the relationship between asymmetry and intelligence (and other variables as well) in the two sexes. This may explain the inconsistent findings in sex differences in asymmetry (see section 10.4.4 of this chapter) and reinforces the need to use sample sizes large enough to test women and men separately with adequate power.

10.1.4 Symmetry and Reaction Time

A similar trend to that of intelligence was observed (in the SFS) between RTs and asymmetry. Children with faster choice RTs exhibited significantly lower asymmetry ($\beta = .17$ and $\beta = .16$ for the first and second samples respectively) and in study 2, children with more consistent choice RTs exhibited lower asymmetry ($\beta = .22$). There were no significant associations between simple RTs with respect to mean scores or intra-individual variability.

As was the case in chapter 4 (asymmetry across childhood), this work was important as it expanded upon an extremely limited body of pre-existing research. No prior work on asymmetry and RTs had been conducted in children. The two prior studies in the area (Penke, et al., 2009; Thoma, et al., 2006) provided some support for links between asymmetry and RTs in adults. Penke et al. found an association between higher facial asymmetry and slower and more variable choice RTs, but no association with simple RTs. Thoma et al. found more asymmetrical men exhibited slower RTs for both simple and choice exercises. This inconsistency cannot be explained by the present work, but it does demonstrate that at least some aspects of RTs are associated with asymmetry and for the first time the work has been extended to children. Note again, however, that effect sizes in the prior studies were relatively high. Thoma et al. has already been described in section 10.1.4; Penke et al. found effect sizes of (r) .3 and .21 for choice mean and variability scores, higher than those found in the present study. Further research would again clarify the expected size of the relationship.

10.1.5 Symmetry and Minor Physical Anomalies

MPAs can be recorded alongside symmetry measures. In the Lothian Birth Cohort 1921 (LBC1921) a more severe finger curvature anomaly was associated with relatively more severe cognitive decline between age 11 and age 79, and between age 11 and age 83 ($\beta = -.18$ and $\beta = -.19$ respectively).

Among children MPAs have previously been linked to intelligence (Pine, et al., 1997; Rosenberg & Weller, 1973), and among those with psychotic disorders, decline in intelligence over time (Dimambro, et al., 2008). This was partially replicated: more severe finger curvature anomalies were associated with greater cognitive decline, but were not associated with intelligence. The use of a continuous measure of severity was useful and had not been attempted in past work. An expansion of symmetry measures to other body parts would, as a byproduct, allow for further MPAs to be measured and incorporated into an MPA mean score or possibly a composite score including MPAs and asymmetry measures. While such work has not been undertaken, chapter 7 demonstrates it is plausible and may provide a useful avenue for improving the reliability of asymmetry work in future as well as partially supporting the evidence in chapter 1 section 1.7 that MPAs independently predict cognitive attributes.

10.1.6 Symmetry and Personality

Using two samples with a combined sample size of 380, no consistent links were found between asymmetry and any of the big five personality traits. This was true for linear and curvilinear relationships, and while there were some significant associations (linearly, with Openness to Experience and Conscientiousness) given the number of tests it is plausible to regard these as type 1 errors.

Again the present work considerably expanded upon the existing studies (Fink, et al., 2005; Pound, et al., 2007; Shackelford & Larsen, 1997) which collectively tested around 500 participants. The work described in chapter 8 represented a considerable increase in sample size compared to the largest prior study. The findings in chapter 8, however, did not agree with the past work. While some authors (Pound, et al., 2007) had expressed concern over the possibility that the findings in the area may have been false positives, this has been far more clearly discussed – and supported – by the present work. The lack of consistency across the

existing studies (including chapter 8) supports the proposal that the prior findings are type 1 errors and that personality has no linear or curvilinear associations with fitness (Penke, et al., 2007).

10.1.7 Symmetry and Socioeconomic Status

For men only, early, but not midlife SES was associated with late life facial asymmetry (standardized path coefficient of $-.44$ in the final model). Tested via a structural equation model, midlife SES had no association with late life facial asymmetry even when the effect of early life SES was constrained to 0. Early life SES has a unique contribution to late life asymmetry.

This finding is in line with work examining illness and SES. Empirical work has demonstrated that poor early life circumstances influence late life health regardless of events in midlife (Barker, 1995). However, the past evidence specifically related to asymmetry is extremely sparse. No prior work has examined the relative contributions of early and midlife to facial asymmetry in late life. The present work is extremely important in demonstrating that asymmetry can be used in parallel with other indicators of wellbeing (such as direct indicators of health).

One prior study did examine facial asymmetry and SES in adolescents (Özener & Fink, 2010). This study also found those living in more adverse conditions exhibited higher facial asymmetry. While the work did not extend to midlife circumstances, along with the present work it demonstrates SES may influence asymmetry.

10.2 Summary of findings

The present work represents a considerable expansion on the existing literature in the field of symmetry research. Through the use of large pre-existing cohorts as well as new data collection in the form of the SFS, the work generated first or near-first empirical accounts of the association between asymmetry and important cognitive and behavioural variables. However, this was only one aspect of the project. The second area of innovation was methodological. This topic will now be discussed.

10.3 Methodological Innovations

Prior research indicated digital measurement of asymmetry traits were preferable due to increased reliability (Kemper & Schwerdtfeger, 2009). The present work further demonstrated the utility of digital measurement: intraclass correlation coefficients (as elsewhere, type 3 was used) of repeated measurements of the hand and bone scans were very high ($r = .90$ or above). Where reliability is high, it is unnecessary to remeasure all traits (Knierim, et al., 2007) and so the work required to measure a sample for asymmetry is reduced.

Importantly, as described in chapter 1 section 1.2.2 and chapter 2, the participant does not need to be present for measurement. As demonstrated in chapter 5, in at least some cases, symmetry scores can be obtained from images not originally intended for research into symmetry. Chapters 4 and 6 demonstrate that symmetry measures are obtainable from hand scans alone. This allows for the recruitment of large samples rapidly (as in the SFS) or acquisition of symmetry measures from large existing cohorts where hand, bone, or face images already exist. Given the proposal that sample sizes must routinely exceed 100 to be useful (Van Dongen & Gangestad, 2011), a claim based on the typically small effect sizes observed, this may be crucial in consistently producing work based on sufficiently large samples.. The evidence in the empirical chapters further demonstrates that methods of acquiring large sample sizes conveniently will be important to further advance research in the field. The use of digital measurement is one method of ensuring this can be done.

As described in chapter 2, it is possible to train volunteers to measure hand scans (and therefore potentially other digital scans) rapidly. With use of appropriate software (again described in chapter 2) this can be efficiently audited and guidance can easily be provided where errors occur. In this fashion, large numbers of images can be rapidly processed by a group of volunteers. This is a further method of rapidly scoring large samples on asymmetry.

Finally, chapter 5 piloted the use of asymmetry of the bones and linked this asymmetry to intelligence. As indicated in chapter 1 section 1.2.1, trait aggregation often reflects convenience (Banks, et al., 2010; Palmer & Strobeck, 1986) and the relative utility of one trait over another remains unclear. Work such as that described in chapter 5 can expand the

range of known usable asymmetry measures and in situations where it is possible to aggregate a large number of asymmetry measures, may improve the validity of the eventual mean asymmetry score (Gangestad & Thornhill, 1999).

10.4 Limitations described in chapter 1

Chapter 1 discussed several outstanding problems in the literature. The empirical work was designed partly as a response to them. The following sections describe how the present work has contributed to overcoming these problems.

10.4.1 Sample Size

Small sample sizes have been a persistent problem in asymmetry research (Banks, et al., 2010; Van Dongen & Gangestad, 2011). The four samples described in the present work all met or exceeded the minimum proposed sample size of Van Dongen and Gangestad (2011): 100 participants. Of the samples, the SFS and the ORCADES both exceeded the recommended sample size of around 350. As reported earlier in this chapter, the observed effect sizes tended to be small to moderate – in line with the findings of recent meta-analyses involving asymmetry (Banks, et al., 2010; Van Dongen & Gangestad, 2011) – and so larger sample sizes are crucial in clarifying what effects exist and the magnitude of them. As noted earlier, one study on intelligence and asymmetry found an extremely large and significant effect size ($r = -.49$) in a sample of only 21 participants. Multiple large studies examining the same topic will allow for clarification of the true size of the effect, whereas many small studies risk exaggerating the effect if only the significant findings achieve publication. As demonstrated in the empirical chapters, effect sizes tend to be small to medium.

As noted in chapter 1, the typical sample size in research on intelligence and asymmetry is relatively small, with the largest previous study exhibiting a sample size of 263 (Johnson, et al., 2008). Chapter 5, with a sample size for the final model of 491, is considerably larger. With the methodological techniques described in section chapter 2 it is possible to repeat such large replications relatively straightforwardly, where scans exist for large cohorts. If

bone scans, hand scans, or facial photographs are available, such work can be conducted even if asymmetry measures were not originally designed to be taken from that cohort.

10.4.2 Diversity of Symmetry Measures and Methods

The present work expanded on symmetry measurement in a number of novel ways. Firstly, it demonstrated clearly that digital measurement was, in terms of time, accessibility, and convenience, preferable to physical measurement. The fact that many pre-existing findings could be replicated from detailed images taken of relatively small areas of the body (such as, in the case of RTs, the hands alone) suggests such measures can be obtained conveniently. This helps avoid the need for comprehensive, time consuming asymmetry procedures for which participants must be present. Just as importantly, the present studies expanded the study of a key variable in symmetry research – intelligence – to endogenous symmetry as measured by the bones. This is extremely useful in several respects. Firstly, it expands the range of usable symmetry measures and suggests the addition of such measures to a composite incorporating external symmetry measures may improve the validity of the final mean asymmetry score. It also demonstrates that bone scans may be used for asymmetry scoring. This expands the range of options for acquiring samples in the future. It also contributes to the issue of how many symmetry measures are needed: With only four measures used to create the mean asymmetry score, and in a design where the experimenter was not aware of the intelligence scores prior to analysis, the association of intelligence and asymmetry identified in past work (Banks, et al., 2010) was still present. This suggests that, with reliable measurement and a large sample, relatively few traits are needed to form a useful asymmetry mean score.

10.4.3 Failure to control for potential confounds

This work demonstrated the importance of controlling for potential confounds in several areas. Age was highlighted in chapters 4 and 5: in the former case in children, in the latter case across adulthood. Age should be accounted for in symmetry research and the present work shows consideration should be given to it when modelling relationships between symmetry and other variables. Notably, symmetry may interact with age in complex way,

such as in chapter 5 where a significant association with age was observed in women but not men. These specific examples illustrate the general need to incorporate age and sex in modelling where they are available, along with testing for the effects of other potential covariates where appropriate. Birth weight and experience of bone breakage were included in the models for chapter 5, but other variables may be pertinent and large cohorts with many measures available are particularly well suited to testing this. Differences in findings in past research may also be due to the tendency to control, or not to control, for certain covariates, or by, for example, comparing samples with very different age ranges without accounting for the impact of age on the model.

10.4.4 Lack of certainty over sex differences

As discussed in chapter 1, there is a lack of clarity on the role of sex differences in asymmetry. Some research has proposed that links between asymmetry and important outcome measures should be stronger among men than among women (Gangestad, et al., 2010) as a result of their greater need to demonstrate fitness. Chapter 1 discussed how this has not consistently been shown and how some authors have used such arguments to exclude women from research in spite of the fact that the issue has not yet been resolved (Banks, et al., 2010).

Sex differences (or the absence of them) have been noted in each empirical chapter. Out of six comparisons for sex differences in asymmetry, two yielded significant results. Problematically, however, three of these comparisons involved children. Restricted to adults only, two of three comparisons resulted in women exhibiting significantly higher levels of asymmetry compared to men. Women also exhibited significantly greater finger curvature anomaly. This evidence is subject to interpretation: treating the child and adult scores as interchangeable and controlling for multiple comparisons leaves only one significant finding. However, the tendency for women to exhibit higher asymmetry and more severe MPAs is important and suggests sample sizes large enough to test men and women separately would be especially useful.

Beyond a comparison of mean scores, there is some evidence from the present work that some variables associate with asymmetry differently according to sex. In chapter 5 the

association between an important outcome measure (age) was significantly larger in women than men, the opposite of what would be predicted if men were expected to exhibit asymmetry clearly as an indicator of fitness. The present work cannot resolve the issue, but it does illustrate that the problem remains important and as such both sexes should be included in research. In particular, the findings in chapter 5 demonstrate that specific variables may influence asymmetry in one sex more than the other, in which case sex differences may be complex and difficult to clarify.

10.5 Limitations in the present work

Limitations in the present work can be grouped into three categories. Firstly, limitations shared by past research, which has already been discussed in depth earlier in this chapter. Secondly, there is the issue of range restriction in some samples making it difficult to establish the genuine effect size. Finally, the symmetry measures used were in some respects limited.

10.5.1 Limitations shared with past research

Of the limitations shared with past research, two stand out as particularly important. Firstly, it was not possible in all samples to control for potential confounds. So, for example, it was possible to control for the effect of birth weight and bone breakage in the ORCADES, but not the SFS. As such the same caution suggested here with regards to past research should be extended to some of the present work. Secondly, the considerable diversity of symmetry measures used is problematic. Given the lack of certainty in how different measures of asymmetry equate to each other, and the inability to, in the present work, establish a consistent set of symmetry measures across all samples the work is reliant upon the assumption that different asymmetry measures are equivalent (Gangestad & Thornhill, 1999). The present work replicated well established findings with novel methods (as in chapter 5) or investigated novel findings with established methods (as in chapters 4 and 6). This provides confidence in the findings. However, a standardized set of measures for all samples would have been preferable to which novel methods could have been added. As has historically

been the case (see chapters 1 and 2) this was not possible due to practical reasons and as such the assumption that the asymmetry measures in each sample are equivalent is assumed, and plausible, but not certain.

10.5.2 Range restriction

Range restriction is not inherently problematic. In some cases (such as in chapter 9) it likely leads to under-estimates, rather than over-estimates of effect sizes and so increases confidence in the genuineness of the relationship. However, it is difficult to establish the magnitude of the effect when the sample exhibits range restriction and two of the samples were restricted or unusual in ways that may have had an important impact on the results. The LBC1921 participants were range restricted in respect to their mid-life attained status (see chapter 9): very few experienced poor circumstances in their midlife. Similarly, the SFS data collected in 2009 suggested the sample was drawn from a much more affluent background than would be representative of the population, with very few from lower SES environments. Given the importance of SES as identified in chapter 9, this range restriction may have decreased certainty in the magnitude of the effect size. Such examples, while not casting doubt on the findings, demonstrate it is difficult to be clear on the genuine size of the effect observed, which in turn makes it difficult to establish what sample sizes are necessary.

10.5.3 Range of symmetry measures

The present work used a variable number of measures. Two samples were particularly notable in using a restricted number or type of measures: the SFS, which used measures taken solely from the hands, and the ORCADES, which used only four bone measures. Traits from areas close to each other on the body may be more likely to exhibit similar levels of asymmetry (Gregory Livshits, et al., 1998) and more measures are usually regarded as preferable (Knierim, et al., 2007). The relevant empirical chapters, and chapter 2, address these issues directly, but it would have been preferable to use a wider range of measures from more traits taken from different areas of the body. The findings in the empirical chapters support the contention that the measures were adequate as in most cases they support past empirical findings or hypotheses. However, if they were suboptimal – and there is at present

no way to tell with certainty – they may have been somewhat unreliable and the effect sizes may, as a consequence, have been under-estimates. Given the practical concerns of data acquisition this was necessary, but as discussed in the preceding section, it is possible the true effect sizes are larger than those given here.

10.6 Future work

Future work arising directly from the present work can take essentially three forms. Firstly, further research could be conducted with the existing samples. Secondly, further research could be conducted on the most under-studied topics identified here. Thirdly, further research could be conducted on comparing different asymmetry measures to each other. Each of these possibilities will now be discussed.

10.6.1 Further research within the existing samples

As described in this chapter, chapter 2, and the relevant empirical chapters, two of the samples used – the LBC1921 and the ORCADES – were large, rich datasets featuring a large number of variables relevant to health, cognition, and wellbeing. As discussed earlier in this chapter, large cohorts allow for large volumes of work on symmetry to be conducted rapidly as no additional data collection beyond the symmetry measures needs to be done to access potentially hundreds of relevant health, behavioural, and cognitive variables. By contrast, small scale studies built around symmetry would require a relatively greater amount of work to access relatively few additional variables also collected by the study designers. Work on behaviour and health was described in chapter 1, but was beyond the scope of the present empirical work. However, such variables remain available in the two samples and a robust set of analyses on physical wellbeing could be conducted with no additional data collection. Given the concern over the ‘broad but shallow’ nature of research on symmetry discussed in chapter 1, even a relatively small number of well-studied cohorts could provide many replications for basic findings, along with the capacity to explore new topics without additional data collection. The LBC1921 and ORCADES are logical starting points.

10.6.2 Further research on under-studied topics

As noted earlier, both chapter 4 and chapter 9 have only one prior study examining their topic. Chapter 6 has two, but none examining children. As such these areas – by contrast to chapter 5 on intelligence – remain understudied. Confidence in the findings would be improved by replications. Given the arguments set out above, and the evidence of the utility of hand scans demonstrated in chapters 4 and 6, acquiring hand or bone scans of child cohorts involved in research on health or wellbeing might provide a straightforward way of expanding the existing work.

10.6.3 Research on asymmetry measures

As noted in chapter 1, chapter 2, and the present chapter, there has been no systematic work identifying how many traits are optimal for an asymmetry mean score, or which traits are most preferable. As noted here and in chapter 5, endogenous asymmetry measures – such as those taken from the bones – may be especially useful as they provide insight into the internal structure of the body rather than superficial external characteristics. This cannot be known with certainty. However, a systematic attempt to identify the minimum number of traits and the most useful traits (if utility differs between traits) would be advantageous. This would enable the optimal use of resources either by avoiding the use of too few measures (which would not provide useful data) or too many (which would waste resources). Recent work has begun to establish clear guidelines on sample size (Banks, et al., 2010; Van Dongen & Gangestad, 2011): parallel work on which measures to use would aid research in this area greatly.

10.6.4 Research on the basis of the associations between asymmetry and well-being

As noted in chapter 1 and elsewhere, the most common explanation for the links between relatively higher asymmetry and relatively poorer scores on a range of outcomes is that asymmetry is indexing underlying well-being. This developmental instability (DI) is a measure of fidelity (Waddington, 1957). Related concepts such as system integrity – a

measure of how well the organism is built (Whalley & Deary, 2001) also provide a plausible account of how high asymmetry comes to be linked to, for example, lower intelligence or slower Reaction Times. However, such theories are untested and vague (Gale, et al., 2009) and the mechanisms are particularly understudied. In chapter 9, explicit mechanisms were suggested including alcohol usage or smoking, but these are speculative. That asymmetry and adverse outcomes are genuinely associated is becoming increasingly clear both because of this work and recent large scale reviews (Banks, et al., 2010; Van Dongen & Gangestad, 2011). The mechanisms that drive the association must now be studied in more detail.

10.7 Conclusions

The present work expanded the literature on asymmetry and its links to cognition and behaviour in several important respects. Across five empirical chapters, the understanding of how asymmetry is related to age, intelligence, RTs, personality, and SES were expanded. A further chapter (7) improved the understanding of how work on MPAs can be fruitfully integrated into research on asymmetry. Methodological improvements – especially the use of digital measurement, the use of pre-existing large cohorts and the expansion of asymmetry measures to include endogenous measures of asymmetry – provide useful avenues for improving future work. Given the breadth of measures available in two of the samples (LBC1921 and ORCADES) further research could conveniently be conducted without additional data collection. Alternatively more work on the understudied topics described in the present work or an expansion of our understanding of existing asymmetry measures would be useful. A clarification of the mechanisms by which the links between asymmetry and adverse outcomes manifest would be especially helpful. In conclusion, the present work demonstrates that symmetry is an important correlate of cognition and behaviour, and evidence of its utility has been demonstrated here across a range of topics.

References

- Alkire, S. (2008). *Concepts and Measures of Agency*. Oxford: OPHI.
- Anderson, J. C., & Gerbing, D. W. (1988). Structural Equation Modeling in Practice: A Review and Recommended Two-Step Approach. *Psychological Bulletin*, 103, 411-423.
- Anderson, N. B., & Armstead, C. A. (1995). Toward understanding the association of socioeconomic status and health: a new challenge for the biopsychosocial approach. *Psychosomatic Medicine*, 57, 213-225.
- Banks, G. C., Batchelor, J. H., & McDaniel, M. A. (2010). Smarter people are (a bit) more symmetrical: A meta-analysis of the relationship between intelligence and fluctuating asymmetry. *Intelligence*, 38, 393-401.
- Barker, D. J. P. (1995). Fetal origins of coronary heart disease. *BMJ*, 311, 171-174.
- Barker, D. J. P. (2007). The origins of the developmental origins theory. *Journal of Internal Medicine*, 261, 412-417.
- Bates, T. C. (2007). Fluctuating asymmetry and intelligence. *Intelligence*, 35, 41-46.
- Bates, T. C., Hope, D. J., Gow, A. J., Pattie, A., Starr, J. M., & Deary, I. J. (submitted for publication). Fluctuating Asymmetry: Developmental precision and human cognition across 76 years.
- Bates, T. C., & Shieles, A. (2003). Crystallized Intelligence as a product of Speed and Drive for Experience: The Relationship of Inspection Time and Openness to "g" and Gc. *Intelligence*, 31, 275-287.
- Bates, T. C., & Stough, C. (1998). Improved Reaction Time Method, Information Processing Speed, and Intelligence. *Intelligence*, 26(1), 53-62.
- Beck, A. T., & Steer, R. A. (1984). Internal consistencies of the original and revised Beck Depression Inventory. *Journal of Clinical Psychology*, 40, 1365-1367.
- Benderlioglu, Z., & Nelson, R. J. (2004). Season of birth and fluctuating asymmetry. *American Journal of Human Biology*, 16(3), 298-310. doi: 10.1002/ajhb.20029
- Benderlioglu, Z., Sciulli, P. W., & Nelson, R. J. (2004). Fluctuating asymmetry predicts human reactive aggression. *American Journal of Human Biology*, 16, 458-469.
- Björklund, A., Jäntti, M., & Solon, G. (2007). Nature and Nurture in the Intergenerational Transmission of Socioeconomic Status: Evidence from Swedish Children and Their Biological and Rearing Parents. *The B.E. Journal of Economic Analysis & Policy*, 7, Article 4.
- Bogin, B. (1997). Evolutionary hypotheses for human childhood. *Yearbook of Physical Anthropology*, 40, 63-89.
- Bogin, B. (2009). Childhood, Adolescence, and Longevity: A Multilevel Model of the Evolution of Reserve Capacity in Human Life History. *American Journal of Human Biology*, 21, 567-577.
- Bradley, R. A., & Srivastava, S. S. (1979). Correlation in Polynomial Regression. *The American Statistician*, 33, 11-14.
- Buss, D. M., & Shackelford, T. K. (2008). Attractive women want it all: Good genes, economic investment, parenting proclivities, and emotional commitment. *Evolutionary Psychology*, 6, 134-146.
- Christensen, H., Mackinnon, A. J., Korten, A., & Jorm, A. F. (2001). The "Common Cause Hypothesis" of Cognitive Aging: Evidence for Not Only a Common Factor but Also Specific Associations of Age With Vision and Grip Strength in a Cross-Sectional Analysis. *Psychology and Aging*, 16, 588-599.
- Compton, M. T., & Walker, E. F. (2009). Physical Manifestations of Neurodevelopmental Disruption: Are Minor Physical Anomalies Part of the Syndrome of Schizophrenia? *Schizophr Bull*, 35, 425-436.
- Costa, P. T., & McCrae, R. R. (1992). *Revised NEO Personality Inventory (NEO-PI-R) and NEO Five-Factor Inventory (NEO-FFI) professional manual*. Odessa, FL: Psychological Assessment Resources.

- Cox, B. D., Huppert, F. A., & Whiclow, M. J. (1993). *The Health and Lifestyle Survey: seven years on*. Aldershot, U.K.: Dartmouth.
- Craik, F. I. M., & Bialystok, E. (2006). Cognition through the lifespan: mechanisms of change. *TRENDS in Cognitive Sciences*, 10, 131-138.
- Daly, M., & Wilson, M. I. (1996). Violence against Stepchildren. *Current Directions in Psychological Science*, 5, 77-81.
- Davey Smith, G., Hart, C., Blane, D., & Hole, D. (1998). Adverse socioeconomic conditions in childhood and cause specific adult mortality: prospective observational study. *BMJ : British Medical Journal*, 316, 1631-1635.
- Deary, I. J. (2008). Why do intelligent people live longer? *Nature*, 456, 175-176.
- Deary, I. J., & Der, G. (2005a). Reaction Time Explains IQ's Association with Death. *Psychological Science*, 16(1), 64-69.
- Deary, I. J., & Der, G. (2005b). Reaction Time, Age, and Cognitive Ability: Longitudinal Findings from Age 16 to 63 Years in Representative Population Samples. *Aging, Neuropsychology, and Cognition*, 12, 187-215.
- Deary, I. J., Der, G., & Ford, G. (2001). Reaction times and intelligence differences: A population-based cohort study. *Intelligence*, 29, 389-399.
- Deary, I. J., Liewald, D., & Nissan, J. (2011). A free, easy-to-use, computer-based simple and four-choice reaction time programme: The Deary-Liewald reaction time task. *Behavior Research Methods*, 43, 258-268. doi: 10.3758/s13428-010-0024-1
- Deary, I. J., Whiteman, M. C., Starr, J. M., Whalley, L. J., & Fox, H. C. (2004). The impact of childhood intelligence on later life: following up the Scottish mental surveys of 1932 and 1947. *Journal of Personality and Social Psychology*, 86, 130-147.
- DeBruine, L. M. (2004). AutoMetric software for measurement of 2D:4D ratios, from www.facelab.org/debruine/Programs/autometric.php
- DeLeon, V. B. (2007). Fluctuating asymmetry and stress in a medieval Nubian population. *American Journal of Physical Anthropology*, 132(4), 520-534. doi: 10.1002/ajpa.20549
- Dimambro, B., Lloyd, T., Dazzan, P., Dean, K., Fearon, P., Doody, G. A., . . . Jones, P. B. (2008). 2 - The association between minor physical anomalies and IQ in first episode psychosis. *Schizophrenia Research*, 98(Supplement 1), 33-33.
- Doyle, O., Harmon, C. P., Heckman, J. J., & Tremblay, R. E. (2009). Investing in early human development: Timing and economic efficiency. *Economics & Human Biology*, 7(1), 1-6.
- Dykiert, D., Der, G., Starr, J. M., & Deary, I. J. (submitted). Sex Differences in Reaction Time Mean and Intra-Individual Variability Across the Life Span.
- Feinberg, A. P., & Irizarry, R. A. (2010). Stochastic epigenetic variation as a driving force of development, evolutionary adaptation, and disease. *Proceedings of the National Academy of Sciences*, 107, 1757-1764. doi: 10.1073/pnas.0906183107
- Fink, B., Neave, N., Manning, J., & Grammer, K. (2005). Facial symmetry and the 'big-five' personality factors. *Personality and Individual Differences*, 39, 523-529.
- Flatt, A. E. (2005). The troubles with pinkies. *Proceedings (Baylor University. Medical Center)*, 18, 341-344.
- Flinn, M., Leone, D., & Quinlan, R. (1999). Growth and Fluctuating Asymmetry of Stepchildren. *Evolution and Human Behavior*, 20(6), 465-479.
- Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-mental state" : A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*, 12, 189-198.
- Frisancho, A. R. (2009). Developmental adaptation: Where we go from here. *American Journal of Human Biology*, 21(5), 694-703. doi: 10.1002/ajhb.20891
- Furlow, F. B., Armijo-Prewitt, T., Gangestad, S. W., & Thornhill, R. (1997). Fluctuating Asymmetry and Psychometric Intelligence. *Proceedings: Biological Sciences*, 264(1383), 823-829.
- Furlow, F. B., Gangestad, S. W., & Armijo-Prewitt, T. (1998). Developmental stability and human violence. *Proceedings of the Royal Society B: Biological Sciences*, 265, 1-6.

- Gale, C. R., Batty, G. D., Cooper, C., & Deary, I. J. (2009). Psychomotor Coordination and Intelligence in Childhood and Health in Adulthood - Testing the System Integrity Hypothesis. *Psychosomatic Medicine*, 71(6), 675-681. doi: 10.1097/PSY.0b013e3181a63b2e
- Gally, E., Kantola-Sorsa, E., & Granström, M.-L. (1988). Intelligence of children of epileptic mothers. *The Journal of pediatrics*, 113(4), 677-684.
- Gangestad, S. W. (2010). Evolutionary biology looks at behavior genetics. *Personality and Individual Differences*, 49, 289-295.
- Gangestad, S. W., Merriman, L. A., & Thompson, M. E. (2010). Men's oxidative stress, fluctuating asymmetry and physical attractiveness. *Animal Behaviour*, 80, 1005-1013.
- Gangestad, S. W., & Thornhill, R. (1997). The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior*, 18, 69-88.
- Gangestad, S. W., & Thornhill, R. (1999). Individual differences in developmental precision and fluctuating asymmetry: a model and its implications. *Journal of Evolutionary Biology*, 12, 402-416.
- Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial Attractiveness, Developmental Stability, and Fluctuating Asymmetry. *Ethology and Sociobiology*, 15, 73-85.
- Geary, D. C., & Bjorklund, D. F. (2000). Evolutionary Developmental Psychology. *Child Development*, 71(1), 57-65.
- General Register Office for Scotland. (2010). *Life Expectancy at Scotland Level*. Retrieved from <http://www.gro-scotland.gov.uk/statistics/theme/life-expectancy/scotland/interim-life-tables.html>.
- Gow, A. J., Johnson, W., Pattie, A., Brett, C. E., Roberts, B., Starr, J. M., & Deary, I. J. (2011). Stability and change in intelligence from age 11 to ages 70, 79, and 87: The Lothian Birth Cohorts of 1921 and 1936. *Psychology and Aging*, 26, 232-240.
- Gow, A. J., Whiteman, M. C., Pattie, A., & Deary, I. J. (2005a). Goldberg's 'IPIP' Big-Five factor markers: Internal consistency and concurrent validation in Scotland. *Personality and Individual Differences*, 39, 317-329.
- Gow, A. J., Whiteman, M. C., Pattie, A., & Deary, I. J. (2005b). The personality-intelligence interface: insights from an ageing cohort. *Personality and Individual Differences*, 39, 751-761.
- Graham, J. H., Emlen, J. M., Freeman, D. C., Leamy, L. J., & Kieser, J. A. (1998). Directional asymmetry and the measurement of developmental instability. *Biological Journal of the Linnean Society*, 64, 1-16.
- Grammer, K., & Thornhill, R. (1994). Human (homo sapiens) facial attractiveness and sexual selection: The role of symmetry and averageness. *Journal of Comparative Psychology*, 108, 233-242.
- Heckman, J. J. (2007). The economics, technology, and neuroscience of human capability formation. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 13250-13255.
- Hope, D., Bates, T. C., Penke, L., Gow, A. J., Starr, J. M., & Deary, I. J. (in press). Symmetry of the face in old age reflects childhood Social Status. *Economics and Human Biology*.
- Huesmann, L. R., Eron, L. D., & Yarmel, P. W. (1987). Intellectual functioning and aggression. *Journal of Personality and Social Psychology*, 52(1), 232-240. doi: 10.1037/0022-3514.52.1.232
- Jasienska, G., Lipson, S. F., Ellison, P. T., Thune, I., & Ziolkiewicz, A. (2006). Symmetrical women have higher potential fertility. *Evolution and Human Behavior*, 27(5), 390-400.
- Jensen, A. R. (1982). Reaction time and psychometric g. In H. J. Eysenck (Ed.), *A Model for Intelligence* (pp. 93-132). Berlin: Springer-Verlag.
- Jensen, A. R. (1992). The importance of intraindividual variation in reaction time. *Personality and Individual Differences*, 13(8), 869-881.
- Jensen, A. R. (1998). *The g factor. The science of mental ability*. Westport, CT.: Praeger.
- Jensen, A. R., & Munro, E. (1979). Reaction time, movement time, and intelligence. *Intelligence*, 3, 121-126.

- Johnson, W., Brett, C. E., & Deary, I. J. (2010). The pivotal role of education in the association between ability and social class attainment: A look across three generations. *Intelligence*, 38, 55-65.
- Johnson, W., Segal, N. L., & Bouchard, T. J. (2008). Fluctuating asymmetry and general intelligence: No genetic or phenotypic association. *Intelligence*, 36, 279-288.
- Just, C. (2011). A review of literature on the general factor of personality. *Personality and Individual Differences*, 50, 765-771. doi: 10.1016/j.paid.2011.01.008
- Kemper, C. J., & Schwerdtfeger, A. (2009). Comparing indirect methods of digit ratio (2D:4D) measurement. *American Journal of Human Biology*, 21, 188-191.
- Kern, M., & Friedman, H. (2008). Do conscientious people live longer? A quantitative review. *Health Psychology*, 27, 505-512.
- Kern, M., Friedman, H., Martin, L., Reynolds, C., & Luong, G. (2009). Conscientiousness, Career Success, and Longevity: A Lifespan Analysis. *Annals of Behavioral Medicine*, 37, 154-163.
- Kieser, J. A., Groeneveld, H. T., & Da Silva, P. C. F. (1997). Dental asymmetry, maternal obesity, and smoking. *American Journal of Physical Anthropology*, 102(1), 133-139. doi: 10.1002/(sici)1096-8644(199701)102:1<133::aid-ajpa11>3.0.co;2-1
- Knierim, U., van Dongen, S., Forkman, B., Tuytens, F. A. M., Spinka, M., Campo, J. L., & Weissengruber, G. E. (2007). Fluctuating asymmetry as an animal welfare indicator -- A review of methodology and validity. *Physiology & Behavior*, 92, 398-421.
- Kobyliansky, E., & Livshits, G. (1989). Age-dependent changes in morphometric and biochemical traits. *Annals of Human Biology*, 16(3), 237-247. doi: doi:10.1080/03014468900000352
- Koga, Y., & Morant, G. M. (1923). On the degree of association between reaction times in the case of different senses. *Biometrika*, 15, 346-372.
- Lang, F. R., Lüdtke, O., & Asendorpf, J. B. (2001). Testgüte und psychometrische Äquivalenz der deutschen Version des Big Five Inventory (BFI) bei jungen, mittelalten und alten Erwachsenen. *Diagnostica*, 47, 111-121.
- Lens, L., Van Dongen, S., Kark, S., & Matthysen, E. (2002). Fluctuating asymmetry as an indicator of fitness: can we bridge the gap between studies? *Biol. Rev.*, 77, 27-38.
- Lezak, M. D. (1995). *Neuropsychological Testing 3rd edition*. Oxford: Oxford University Press.
- Little, B. B., Buschang, P. H., & Malina, M. (2002). Anthropometric asymmetry in chronically undernourished children from Southern Mexico. *Annals of Human Biology*, 29, 526-537.
- Livshits, G., Davidi, L., Kobyliansky, E., Ben-Amitai, D., Levi, Y., Merlob, P., . . . Reynolds, J. F. (1988). Decreased developmental stability as assessed by fluctuating asymmetry of morphometric traits in preterm infants. *American Journal of Medical Genetics*, 29(4), 793-805. doi: 10.1002/ajmg.1320290409
- Livshits, G., Yakovenko, K., Kletselman, L., Karasik, D., & Kobyliansky, E. (1998). Fluctuating asymmetry and morphometric variation of hand bones. *American Journal of Physical Anthropology*, 107, 125-136.
- Lloyd, T., Doody, G., Brewin, J., Park, B., & Jones, P. (2003). Minor physical anomalies in schizophrenia: is age a confounding factor? *Schizophrenia Research*, 61(1), 67-73.
- Ludwig, W. (1932). *Das Rechts-Links Problem in teirrech und beim menschen*. Berlin: Springer.
- Luxen, M. F., & Buunk, B. P. (2006). Human intelligence, fluctuating asymmetry and the peacock's tail General intelligence (g) as an honest signal of fitness. *Personality and Individual Differences*, 41, 897-902.
- Lynch, J. W., Kaplan, G. A., & Salonen, J. T. (1997). Why do poor people behave poorly? Variation in adult health behaviours and psychosocial characteristics by stages of the socioeconomic lifecourse. *Social Science & Medicine*, 44, 809-819.
- Manning, J., Koukourakis, K., & Brodie, D. A. (1997). Fluctuating asymmetry, metabolic rate and sexual selection in human males. *Evolution and Human Behavior*, 18(1), 15-21.
- Manning, J., Scutt, D., & Lewis-Jones, D. I. (1998). Developmental Stability, Ejaculate Size, and Sperm Quality in Men. *Evolution and Human Behavior*, 19, 273-282.
- Manning, J., & Wood, D. (1998). Fluctuating asymmetry and aggression in boys. *Human Nature*, 9, 53-65.

- Marcus, J., Hans, S. L., Byhouwer, B., & Norem, J. (1985). Relationships Among Neurological Functioning, Intelligence Quotients, and Physical Anomalies. *Schizophrenia Bulletin*, 11(1), 101-106. doi: 10.1093/schbul/11.1.101
- Markow, T. A., & Wandler, K. (1986). Fluctuating Dermatoglyphic Asymmetry and the Genetics of Liability to Schizophrenia. *Psychiatry Research*, 19, 323-328.
- Marmot, M. (2010). Fair Society, Healthy Lives: The Marmot Review Final Report: UCL.
- Martin, S. M., Manning, J. T., & Dowrick, C. F. (1999). Fluctuating Asymmetry, Relative Digit Length, and Depression in Men. *Evolution and Human Behavior*, 20(3), 203-214.
- McEwen, B. S., & Stellar, E. (1993). Stress and the Individual: Mechanisms Leading to Disease. *Arch Intern Med*, 153(18), 2093-2101. doi: 10.1001/archinte.1993.00410180039004
- McGeorge, P., Crawford, J. R., & Kelly, S. W. (1996). The relationship between WAIS-R abilities and speed of processing in a word identification task. *Intelligence*, 23, 175-190.
- McMillen, I. C., & Robinson, J. S. (2005). Developmental Origins of the Metabolic Syndrome: Prediction, Plasticity, and Programming. *Physiol. Rev.*, 85, 571-633.
- McQuillan, R., Leutenegger, A.-L., Abdel-Rahman, R., Franklin, C. S., Pericic, M., Barac-Lauc, L., . . . Wilson, J. F. (2008). Runs of Homozygosity in European Populations. *American journal of human genetics*, 83(3), 359-372.
- Mellor, C. S. (1992). Dermatoglyphic Evidence of Fluctuating Asymmetry in Schizophrenia. *British Journal of Psychiatry*, 160, 467-472.
- Milne, B. J., Belsky, J., Poulton, R., Thomson, W. M., Caspi, A., & Kieser, J. (2003). Fluctuating asymmetry and physical health among young adults. *Evolution and Human Behavior*, 24, 53-63.
- Møller, A. P. (2006). A review of developmental instability, parasitism and disease: Infection, genetics and evolution. *Infection, Genetics and Evolution*, 6(2), 133-140.
- Murray, C. J. L., & Lopez, A. D. (1997). Mortality by cause for eight regions of the world: Global Burden of Disease Study. *The Lancet*, 349(9061), 1269-1276.
- Nishiwaki, Y., Clark, H., Morton, S. M., & Leon, D. A. (2005). Early life factors, childhood cognition and postal questionnaire response rate in middle age: the Aberdeen Children of the 1950s study. *BMC Medical Research Methodology*, 5.
- Otremski, I., Katz, M., Livshits, G., & Cohen, Z. (1993). Biology of aging in an Israeli population. 1. Review of literature and morphological variation analysis. *Anthropologischer Anzeiger; Bericht Über Die Biologisch-Anthropologische Literatur*, 51, 233-249.
- Özener, B. (2010). Fluctuating and directional asymmetry in young human males: Effect of heavy working condition and socioeconomic status. *American Journal of Physical Anthropology*, 143, 112-120. doi: 10.1002/ajpa.21300
- Özener, B., & Ertuğrul, B. (2011). Relationship between shortness of final body height and fluctuating asymmetry in Turkish young males. *Annals of Human Biology*, 38(1), 34-38. doi: 10.3109/03014460.2010.486770
- Özener, B., & Fink, B. (2010). Facial symmetry in young girls and boys from a slum and a control area of Ankara, Turkey *Evolution and Human Behavior*, 31, 436-441.
- Ozgen, H. M., Hop, J. W., Hox, J. J., Beemer, F. A., & van Engeland, H. (2010). Minor physical anomalies in autism: a meta-analysis. *Molecular Psychiatry*, 15, 300-307.
- Palmer, A.R. (2004). Symmetry Breaking and the Evolution of Development. *Science*, 306, 828-833.
- Palmer, A. R., & Strobeck, C. (1986). Fluctuating asymmetry: measurement, analysis, patterns. *Annual Review of Ecology and Systematics*, 17, 391-421.
- Paulhus, D. L., & Martin, C. L. (1986). Predicting adult temperament from minor physical anomalies. *Journal of Personality and Social Psychology*, 50, 1235-1239.
- Penke, L., & Asendorpf, J. B. (2008). Beyond Global Sociosexual Orientations: A More Differentiated Look at Sociosexuality and Its Effects on Courtship and Romantic Relationships. *Journal of Personality and Social Psychology*, 95, 1113-1135.
- Penke, L., Bates, T. C., Gow, A. J., Pattie, A., Starr, J. M., Jones, B. C., . . . Deary, I. J. (2009). Symmetric faces are a sign of successful cognitive aging. *Evolution and Human Behavior*, 30, 429-437.

- Penke, L., Denissen, J. J. A., & Miller, G. F. (2007). The Evolutionary Genetics of Personality. *Eur. J. Pers*, 21, 549–587.
- Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. I., Rowland, D. A., & Edwards, R. (1999). Symmetry and Human Facial Attractiveness. *Evolution and Human Behavior*, 20, 295–307.
- Pine, D. S., Shaffer, D., Schonfeld, I. S., & Davies, M. (1997). Minor Physical Anomalies: Modifiers of Environmental Risks for Psychiatric Impairment? *Journal of the American Academy of Child & Adolescent Psychiatry*, 36(3), 395–403.
- Pound, N., Penton-Voak, I. S., & Brown, W. M. (2007). Facial symmetry is positively associated with self-reported extraversion. *Personality and Individual Differences*, 43, 1572–1582.
- Prokosch, M. D., Yeo, R. A., & Miller, G. F. (2005). Intelligence tests with higher g-loadings show higher correlations with body symmetry: Evidence for a general fitness factor mediated by developmental stability. *Intelligence*, 33(2), 203–213.
- Rahman, Q., Wilson, G. D., & Abrahams, S. (2004). Developmental Instability Is Associated With Neurocognitive Performance in Heterosexual and Homosexual Men, but Not in Women. *Behavioral Neuroscience*, 118, 243–247.
- Reilly, J. L., Murphy, P. T., Byrne, M., Larkin, C., Gill, M., O'Callaghan, E., & Lane, A. (2001). Dermatoglyphic fluctuating asymmetry and atypical handedness in schizophrenia. *Schizophrenia Research*, 50, 159–168.
- Rhodes, G., Zebrowitz, L. A., Clark, A., Kalick, S. M., Hightower, A., & McKay, R. (2001). Do facial averageness and symmetry signal health? *Evolution and Human Behavior*, 22(1), 31–46.
- Roberts, B. A., Der, G., Deary, I. J., & Batty, G. D. (2009). Reaction time and established risk factors for total and cardiovascular disease mortality: Comparison of effect estimates in the follow-up of a large, UK-wide, general-population based survey. *Intelligence*, 37(6), 561–566.
- Roberts, B. W., & Mroczek, D. (2008). Personality trait change in adulthood. *Current directions in psychological science: a journal of the American Psychological Society*, 17(1), 31.
- Rosenberg, J. B., & Weller, G. M. (1973). Minor Physical Anomalies and Academic Performance in Young School-children. *Developmental Medicine & Child Neurology*, 15(2), 131–135. doi: 10.1111/j.1469-8749.1973.tb15152.x
- Rushton, J. P. (1990). Sir Francis Galton, Epigenetic Rules, Genetic Similarity Theory, and Human Life-History Analysis. *Journal of Personality*, 58, 117–140.
- Scottish Council for Research in, E. (1933). *The Intelligence of Scottish Children: A National Survey of an Age-Group*. London: University Press.
- Seeman, T., Epel, E., Gruenewald, T., Karlamangla, A., & McEwen, B. S. (2010). Socio-economic differentials in peripheral biology: Cumulative allostatic load. *Annals of the New York Academy of Sciences*, 1186, 223–239.
- Sen, A. (1999). *Commodities and Capabilities*. New Delhi: Oxford University Press.
- Shackelford, T. K., & Larsen, R. J. (1997). Facial asymmetry as an indicator of psychological, emotional, and physiological distress. *Journal of Personality and Social Psychology*, 72, 456–466.
- Shrout, P.E., & Fleiss, J.L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin*, 86, 420–428.
- Simmons, L. W., Rhodes, G., Peters, M., & Koehler, N. (2004). Are human preferences for facial symmetry focused on signals of developmental instability? *Behavioral Ecology*, 15, 864–871.
- Sivkov, S. T., & Akabaliev, V. H. (2003). Minor physical anomalies in mentally healthy subjects: Internal consistency of the Waldrop Physical Anomaly Scale. *American Journal of Human Biology*, 15(1), 61–67.
- Smith, D. W. (1970). *Recognizable patterns of human malformation*. Philadelphia: W.B. Saunders.
- Sokka, T., Toloza, S., Cutolo, M., Kautiainen, H., Makinen, H., Gogus, F., . . . the, Q.-R. A. G. (2009). Women, men, and rheumatoid arthritis: analyses of disease activity, disease characteristics, and treatments in the QUEST-RA Study. *Arthritis Research & Therapy*, 11, R7.
- Spearman, C. (1927). *The abilities of man*. New York NY: Macmillan.
- SPSS Inc. (2010). AMOS 18.00 (Build 992). Chicago: SPSS Inc.

- Starr, J. M., Kilgour, A., Pattie, A., Gow, A. J., Bates, T. C., & Deary, I. J. (2010). Height and intelligence in the Lothian Birth Cohort 1921: a longitudinal study. *Age and Ageing*, 39, 272-275.
- Thoma, R. J., Yeo, R. A., Gangestad, S. W., Halgren, E., Davis, J., Paulson, K. M., & Lewine, J. D. (2006). Developmental instability and the neural dynamics of the speed-intelligence relationship. *NeuroImage*, 32(3), 1456-1464.
- Thornhill, R., & Gangestad, S. W. (1994). Human Fluctuating Asymmetry and Sexual Behavior. *Psychological Science*, 5, 297-302.
- Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior*, 27, 131-144.
- van Dongen, S. (2011). Associations between asymmetry and human attractiveness: Possible direct effects of asymmetry and signatures of publication bias. *Annals of Human Biology*, 38(3), 317-323.
- van Dongen, S., Cornille, R., & Lens, L. (2009). Sex and asymmetry in humans: what is the role of developmental instability? *Journal of Evolutionary Biology*, 22, 612-622.
- Van Dongen, S., & Gangestad, S. W. (2011). Human fluctuating asymmetry in relation to health and quality: a meta-analysis. *Evolution and Human Behavior*, 32, 380-398.
- Van Dongen, S., Wijnaendts, L. C. D., Ten Broek, C. M., & Galis, F. (2009). Fluctuating Asymmetry does not consistently reflect severe developmental disorders in human fetuses. *Evolution*, 63(7), 1832-1844. doi: 10.1111/j.1558-5646.2009.00675.x
- van Valen, L. (1962). A Study of Fluctuating Asymmetry. *Evolution*, 16(2), 125-142.
- Waddington, C. H. (1957). *The strategy of the genes*. London: Allen and Unwin.
- Waldrop, M. F., Pedersen, F. A., & Bell, R. Q. (1968). Minor physical anomalies and behavior in preschool children. *Child Development*, 39, 391-400.
- Waynforth, D. (1998). Fluctuating asymmetry and human male life-history traits in rural Belize. *Proceedings of the Royal Society B: Biological Sciences*, 265, 1497-1501.
- Wechsler, D. (1998a). *WAIS-IIIUK administration and scoring manual*. London: Psychological Corporation.
- Wechsler, D. (1998b). *WMS-IIIUK administration and scoring manual*. London: Psychological Corporation.
- Weinberg, S. M., Jenkins, E. A., Marazita, M. L., & Maher, B. S. (2007). Minor physical anomalies in schizophrenia: a meta-analysis. *Schizophrenia Research*, 89(1-3), 72-85.
- Weinstein, D. D., Diforio, D., Schiffman, J., Walker, E., & Bonsall, R. (1999). Minor Physical Anomalies, Dermatoglyphic Asymmetries, and Cortisol Levels in Adolescents With Schizotypal Personality Disorder. *Am J Psychiatry*, 156(4), 617-623.
- Whalley, L. J., & Deary, I. J. (2001). Longitudinal cohort study of childhood IQ and survival up to age 76. *BMJ*, 322(7290), 819.
- Wilkinson, R. T., & Allison, S. (1989). Age and simple reaction time: Decade differences for 5,325 subjects. *Journal of Gerontology: Psychological Sciences*, 4, 29-35.
- Williams, P. G., O'Brien, C. D., & Colder, C. R. (2004). The effects of neuroticism and extraversion on self-assessed health and health-relevant cognition. *Personality and Individual Differences*, 37(1), 83-94.
- Wilson, J. M., & Manning, J. (1996). Fluctuating asymmetry and age in children: evolutionary implications for the control of developmental stability. *Journal of Human Evolution*, 30, 529-537.
- Zaatari, D., Palestis, B. G., & Trivers, R. (2009). Fluctuating Asymmetry of Responders Affects Offers in the Ultimatum Game Oppositely According to Attractiveness or Need as Perceived by Proposers. *Ethology*, 115(7), 627-632. doi: 10.1111/j.1439-0310.2009.01648.x
- Zaatari, D., & Trivers, R. (2007). Fluctuating asymmetry and behavior in the ultimatum game in Jamaica. *Evolution and Human Behavior*, 28, 223-227.